



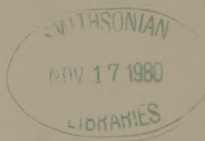


ANNALS OF THE
SOUTH AFRICAN MUSEUM

ANNALE VAN DIE
SUID-AFRIKAANSE MUSEUM

VOLUME 81

BAND 81



ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

VOLUME 81 BAND



THE TRUSTEES OF THE
SOUTH AFRICAN MUSEUM
CAPE TOWN

DIE TRUSTEES VAN DIE
SUID-AFRIKAANSE MUSEUM
KAAPSTAD

1980

SET, PRINTED AND BOUND IN THE REPUBLIC OF SOUTH AFRICA BY
THE RUSTICA PRESS (PTY.) LTD., WYNBERG, CAPE

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FEBRUARY 1980

ISSN 0303-2515

ANNALS

OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN



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Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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The number of the figure should be lightly marked in pencil on the back of each illustration.

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- 'As described (Haughton *et al.* 1927) . . .'

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'*et al.*' in text for more than two joint authors, but names of all authors given in list of references.

(b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc. to the year for more than one paper by the same author in that year, e.g. Smith (1969a, 1969b) and not Smith (1969, 1969a).

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BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.

FISCHER, P.-H. 1948. Données sur la résistance et de la vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.

FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.

KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.

KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.

THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270.

Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume 81 Band
February 1980 Februarie
Part 1 Deel



AGRIOTHERIUM (MAMMALIA, URSIDAE) FROM
LANGEBAANWEG, SOUTH AFRICA, AND
RELATIONSHIPS OF THE GENUS

By

Q. B. HENDEY

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town 8000

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na gelang van die
beskikbaarheid van stof

Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad 8000

OUT OF PRINT/UIT DRUK

1, 2(1-3, 5-8), 3(1-2, 4-5, 8, t.-p.i.), 5(1-3, 5, 7-9),
6(1, t.-p.i.), 7(1-4), 8, 9(1-2, 7), 10(1-3),
11(1-2, 5, 7, t.-p.i.), 15(4-5), 24(2), 27, 31(1-3), 32(5), 33

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Kopieregnavrae aan die Suid-Afrikaanse Museum

ISBN 0 908407 84 X

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

AGRIOTHERIUM (MAMMALIA, URSIDAE) FROM LANGEBAANWEG, SOUTH AFRICA, AND RELATIONSHIPS OF THE GENUS

By

Q. B. HENDEY

South African Museum, Cape Town

(With 42 figures and 21 tables)

[MS. accepted 11 September 1979]

ABSTRACT

Agriotherium africanum from the latest Miocene/early Pliocene Varswater Formation at Langebaanweg, and other relevant material indicate that *Agriotherium* was descended from late Miocene *Indarctos*. Later Ursidae are divided into the subfamilies Ursavinae (*Ursavus* spp), Agriotheriinae (tribes Agriotheriini and Ailuropodini), and Ursinae (Ursini and Tremarctini). '*Ursavus*' *depereti* and *Ailuropoda melanoleuca* constitute the Ailuropodini, and *Indarctos* and *Agriotherium* the Agriotheriini. The latter consist of a primary European lineage from which branches in Africa, Asia and North America arose. Either all species of *Indarctos*, or the later ones only, should perhaps be referred to *Agriotherium*.

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INTRODUCTION

Agriotherium africanum from the latest Miocene/early Pliocene Varswater Formation exposed in a phosphate mine ('E' Quarry) at Langebaanweg, Cape Province (Fig. 1), was the first member of its genus to be recorded in Africa, and the first bear known from sub-Saharan Africa (Hendey 1972; Wolff *et al.* 1973). Although the first *Agriotherium* specimens were found in Europe at least as long ago as 1809 (Stehlin 1907), and others have since been collected at scattered localities through much of the Old World and North America, this genus has remained relatively poorly known, being represented for the most part by fragmentary material belonging to few individuals.

Initially this also applied to the Langebaanweg representative of the genus, but later more material came to light and it is remarkable that '*Agriotherium africanum*, the most recently described and most remote record of the genus, is apparently also the best represented' (Hendey 1977: 112). It is in the latter

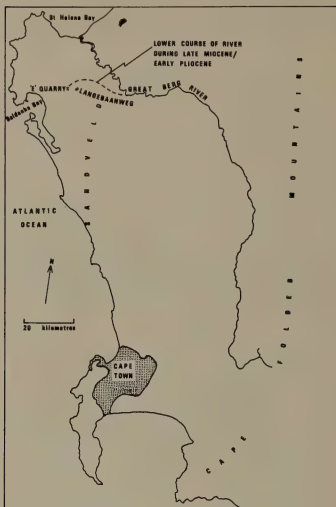


Fig. 1. The south-western Cape Province.

respect that *A. africanum* is particularly noteworthy. It provides the best indication yet that *Agriotherium*, like other bears, was characterized by appreciable variation in its dentition and in size, the latter evidently being due to marked sexual dimorphism.

A. africanum specimens are recorded from two stratigraphic horizons in 'E' Quarry, namely beds 3aS and 3aN of the Pelletal Phosphorite Member (Hendey 1976). The bed 3aS sample, which includes the holotype, comprises only a small part of the total assemblage. Most of the bed 3aN sample was collected in a restricted area (the fossil accumulation at Locality 5—Dingle *et al.* 1979, fig. 2). This material is from a river channel lag deposit, which was laid down in the lee of a phosphate rock outcrop, while the remainder of the bed 3aN sample was from lateral extensions of the lag deposit. Since this material was probably accumulated during a very restricted period, the bed 3aN

A. africanum sample may represent remnants of a single population in a temporal as well as a geographical sense. There is no reason to believe that the character diversity observed in this sample can be ascribed to anything but normal intra-specific variation.

On the other hand, there are differences between bed 3aS and bed 3aN specimens which apparently reflect evolutionary changes, suggesting that the time interval between deposition of these beds was of sufficient duration for such changes to have occurred. The differences are, however, insufficient to warrant formal nomenclatural recognition. *A. africanum* thus joins the growing number of species which indicate that deposition of the Varswater Formation took place over an appreciable period in time (see Hendey 1978; Gentry 1980). Langebaanweg is the only recorded locality where *Agriotherium* is known to occur in more than one stratigraphic horizon.

A. africanum is also of interest since it is one of several species now known from sub-Saharan Africa which indicate that towards the end of the Miocene this region had closer faunal links with Eurasia (Hendey 1978). The present study of *Agriotherium* has suggested that faunal interchange at this time was between Africa and Europe, presumably by way of an Iberian/north-west African connection, rather than, or in addition to, one between Africa and Asia via the Middle East. Apart from *A. africanum*, the Langebaanweg carnivores, *Plesiogulo monspessulanus* and *Dinofelis diastemata*, also point to such a connection, as have recent studies on other mammals (e.g. Forstén 1978).

Until the recent discovery of an agriotheriine at Sahabi in Libya (Boaz *et al.* 1979), the Langebaanweg *Agriotherium* was the only African record of the group, and its location at the southern continental extremity was evidence that it had been widespread on this continent.

On a more mundane level, *A. africanum* has an appeal in that it is still South Africa's only known bear, living or fossil.

The material described below is housed in the South African Museum, and catalogue numbers are prefixed SAM-PQ-, which identifies the institution and department concerned. This lettering is omitted from the text, and the locality prefix (L) and serial numbers of specimens only are given. Modern comparative material in this museum is distinguished by the prefix ZM.

Other institutional abbreviations used in the text are as follows:

BMNH—British Museum (Natural History), London

GSI —Geological Survey of India, Calcutta

NMB —Naturhistorisches Museum, Basel

NMW —Naturhistorisches Museum, Vienna

Originals and casts of *Agriotherium* and related taxa in, or from, the above institutions were examined in the course of the present study. In addition, skulls and skeletons of extant ursids in the South African Museum and the British Museum (Natural History) were studied. Comparative data were otherwise obtained from the publications cited.

THE LANGEBAANWEG *AGRIOTHERIUM*

MATERIAL

The available *Agriotherium africanum* specimens are listed below according to the horizon from which they were derived, and, where possible, according to sites or areas within 'E' Quarry.

Pelletal Phosphorite Member, bed 3aS

L2045—Left maxillary fragment with P⁴ (holotype)

L1868—Left I₁, right P³, fragments of right P⁴ and M¹

L1844, L3141—Left I₂ and I₃, probably of the same individual (Wolff *et al.* (1973) were incorrect in identifying L1844 as a right I₁)

L12637—Incomplete left M¹ (Hendey (1972) was incorrect in identifying this tooth as M²)

L2154—Incomplete proximal left ulna

The above specimens were described or discussed by Hendey (1972) and Wolff *et al.* (1973).

L12561—Right M₃ (see Hendey 1972)

L12033, L41270—Right I³'s

L40031—Left hemimandible fragment and distal left humerus

L40030—Right metatarsal II and 2nd phalanx, probably of same individual as L40031

L40002—Left femur and patella, and a thoracic vertebra, of one individual

L3433—Left humerus lacking proximal parts

L3994—Shaft of left humerus

L40040—Distal right humerus

L12383—Proximal right ulna

L40003—Left radius lacking distal parts

L41702—Left scapholunar

L41295—Right cuneiform

L12503—Right pisiform

L20998, L25862—Right metacarpals III

L41575—Right metacarpal IV

L40043, L40128—Proximal right and left femora

L40028, L40029—Proximal right tibiae

L41108—Proximal right metatarsal V

L10411—Proximal 1st phalanx

L42667—2nd phalanx

The above material represents at least three individuals, but since the specimens were collected over a wide area and from different levels within bed 3aS, the actual number is certainly much higher. Unless otherwise stated, each catalogue number could represent a different individual, which makes a total of 28.

It is not certain that those specimens in this series with numbers above L40000 are all from bed 3aS (see p. 62).

Pelletal Phosphorite Member, bed 3aN—excavation LBW-E 1975/1 (site—TCWW Prom)

L33160—Incomplete left manus, comprising scapholunar, unciform, magnum, trapezoid and metacarpals II to V, the latter lacking distal ends and some of the carpals incomplete

L33341, L34188—Incomplete right and left innominates

L30205—Left metatarsal III

L33557—Proximal left metatarsal V

The above material represents at least 2 individuals.

Pelletal Phosphorite Member, bed 3aN—excavation LBW-E 1976/1 (site—RP)

L33824—Crown of left \underline{C} .

L33825—Left I_3

L13826—Proximal right radius

L33828—Right metacarpal IV

L33830—Distal metapodial fragment

The above material represents at least one individual.

Pelletal Phosphorite Member, bed 3aN—excavation LBW-E 1976/2 (site—IWRP or Locality 5 of Dingle et al. 1979)

L45062—Incomplete skull (partly restored) and mandible (restored), lacking left I^1 , right I^3 , left and right P^1 , right lower incisors, and left P_3

Associated postcranial bones, including: parts of at least 7 vertebrae (some numbered L49048 and L49115); fragment of distal right humerus; right ulna lacking distal parts; right scapholunar, cuneiform, pisiform, unciform, magnum and trapezoid; proximal right metacarpal III; proximal left humerus; left ulna with distal parts detached and fragmented; left radius lacking part of shaft; right tibia and proximal fibula; right astragalus, calcaneum, navicular and cuboid; right metatarsals II, IV and V; left astragalus; left metatarsal III and proximal metatarsal II; 11 sesamoids, five 1st phalanges, four 2nd phalanges and four 3rd phalanges

L45137—Right I^2 , \underline{C} lacking root, and P^4 to M^2 ; left \underline{C} and P^4 to M^2 ; some skull fragments

L45114—Right hemimandible lacking ascending ramus, incisors, P_3 and M_3

The above specimens were briefly discussed by Hendey (1977).

L46605, L48564, L48577—Left and right maxillary fragments with M^2 's and part of left M^1

L46573—Crown of right I^2

L47758/9—Right and left I^3 , probably of the same individual

L48851—Fragment of left I^3

L46074—Right P^4

L47698—Left M^2

L46563—Left M_2 , probably of same individual as L45114

L48742—Fragment of mandibular condyle

- L47449, L47701, L47830—Incomplete cervical vertebrae
 L45063—Incomplete left forelimb, comprising humerus (partly restored), with proximal end detached; ulna and radius (restored); scapholunar, cuneiform, pisiform, unciform, magnum, trapezoid and trapezium; metacarpal, V, and fragments of metacarpals I, III and IV; three sesamoids; three 1st phalanges
 L46602—Proximal left humerus
 L48741, L48747—Proximal left radii
 L47699/700—Proximal left and right radii of one individual
 L46076—Right ulna lacking distal end
 L46134—Left scapholunar, right pisiform and metapodial fragment, probably of one individual
 L46132, L48021—Left and right scapholunars
 L47074—Right magnum
 L45448—Left metacarpal I and distal metapodial fragment, probably of one individual
 L48432—Right metacarpal IV
 L49889—Distal left femur
 L47533, L47910—Left and right astragali
 L47387—Proximal right metatarsal I
 L48572/3—Right metatarsal V and left metatarsal II, probably of one individual
 L46133, L46216, L48766—Metapodial fragments
 L47358, L48533, L48730, L49888—1st phalanges
 L48213, L48230—2nd phalanges

The above material represents at least five individuals.

Pelletal Phosphorite Member, bed 3aN—surface finds in the vicinity of LBW-E 1976/2

- L47242—Left premaxilla and right M² of one individual.
 L50636—Right I³
 L50981—Left M₃
 L42537—Proximal left ulna and distal femur, lacking epiphyses, of one individual
 L50635—Left scapholunar
 L50638—Patella
 L50637—Distal metapodial
 L41468—1st phalanx

The above material represents at least two individuals.

Pelletal Phosphorite Member, bed 3aN—dump 10 sample from deposits immediately north of LBW-E 1976/2

- L55012—Left and right P⁴'s and right M¹ of one individual
 L55015, L55016—Right I²'s
 L55014—Left I³

- L55013—Crown of right \bar{C}
- L55017—Four anterior premolars of more than one individual
- L55029—Right metacarpal I
- L55019—Distal left fibula
- L55021—Right navicular
- L55022/28—Seven metapodial fragments
- L55020—Sesamoid
- L55030/35—Six 1st phalanges
- L55036—2nd phalanx
- L55037/43—Seven 3rd phalanges

The above material represents at least two individuals.

Pelletal Phosphorite Member, bed 3aN—dump 9 sample from deposits immediately west of LBW-E 1976/2

- L50445—Incomplete left hemimandible with \bar{C} and P_4
- L50453—Fragment of left P^4
- L50458—Right I_2
- L50446—Right M_1
- L50457—Left magnum
- L50454—Distal metapodial fragment
- L51592—2nd phalanx
- L50455/6—Two 3rd phalanges

The above material represents at least one individual.

Pelletal Phosphorite Member, bed 3aN—dump 8 sample from deposits immediately south of LBW-E 1976/2

- L50003—Incomplete left hemimandible with P_4 and M_2
- L50004—Incomplete left hemimandible with P_4 and associated M_1 and M_2
- L50903—Fragments of right hemimandible with incomplete \bar{C}
- L50008—Incomplete right P^4
- L50005/6—Right and left M_1 's
- L50007—Right M_2

Unnumbered teeth and tooth fragments, including right I^2 , I^3 and I_1 , a canine and two anterior premolars

- L50843/54—Eleven vertebra fragments
- L50857/8—Incomplete left and right scapulae
- L50834/5/6/8/9—Humerii fragments of at least two individuals
- L50806, L50816—Proximal left and right radii
- L50807—Distal right radius fragment
- L50777—Distal epiphysis of right radius
- L50763—Left ulna lacking distal end
- L50764—Left ulna fragment
- L50840—Proximal ulna fragment

- L50805, L50808—Distal right ulnae
- L50767—Right scapholunar
- L50813, L50819—Fragments of right and left scapholunars, probably of one individual
- L50786, L50795—Left and right cuneiforms
- L50772, L50774—Right unciforms
- L50791, L50794—Right magnums
- L50775—Left metacarpal I
- L50783, L50788—Left and right metacarpals III
- L50810—Proximal right metacarpal III
- L50855/6/9/60—Femora fragments of at least two individuals
- L50841, L50833—Proximal and distal left tibia, probably of one individual
- L50842—Proximal right tibia
- L50769—Distal epiphysis of right tibia
- L50815, L50828—Distal left and right fibulae
- L50765/6—Left astragali
- L50770, L50789—Right astragali
- L50768—Right calcaneum lacking tuber calcis epiphysis
- L50773—Left navicular
- L50778, L50790—Right and left entocuneiforms
- L50771, L50787—Left and right metatarsals I
- L50824—Proximal left metatarsal IV
- L50812, L50829—Proximal right metatarsals V
- L50809/11/14/17/18/20/22/23/25/26/30—Eleven metapodial fragments
- L50802—Sesamoid
- L50776/80/81/84/93/97—Six 1st phalanges
- L50821/7—Two incomplete 1st phalanges
- L50785/96/804—Three 2nd phalanges
- L50782/98/99/800/801—Five 3rd phalanges
- L50831—Incomplete 3rd phalanx

The above material represents at least four individuals.

Pelletal Phosphorite Member, bed 3aN—carbonaceous deposit south of dump 8 area

- L41404—Fragmented and incomplete skull, with only the left premaxilla and maxilla largely intact, and with right ?P², and left C (damaged), P⁴, M¹ and M² (see Hendey 1977)
- L40044—Mandible fragment with associated right radius and fragments of ulna
- L43126—Fragments of at least six thoracic and lumbar vertebrae.

The above material represents at least two individuals.

The minimum number of individuals represented in the combined bed 3aN samples is eleven, although the actual number may be far higher. These samples are from a single horizon of river channel and associated deposits, which were exposed over a linear distance of about 200 m, with sample areas either contiguous

or not far removed from one another. Elements of individual skeletons are likely to be represented in more than one sample unit.

THE SKULL

Apart from L45062, the only other described skull of *Agriotherium* is one belonging to *A. sivalense* from the Siwalik Hills in India (Falconer & Cautley 1836; Lydekker 1884). Both skulls are incomplete, and although L45062 is also slightly distorted in parts, it is perhaps the more informative of the two specimens. They are similar in overall size, and, in so far as comparisons are possible, they are also similar in morphology.

Another skull which is remarkably like that of the Langebaanweg *Agriotherium* is of an *Indarctos* from Florida which was recently described by Wolff (1978). Although the Langebaanweg and Florida skulls undoubtedly do belong to *Agriotherium* and *Indarctos* as these genera are presently conceived, the description of skull characters in the latter (Wolff 1978: 2-4) could, with only slight modification, serve as a description of the Langebaanweg specimen. The significance of this will be discussed later (see p. 93).

Other described skulls of *Indarctos*, of which there are two from Samos (Helbing 1932; Thenius 1949, 1959) and one from Spain (Crusafont & Kurtén 1976), are less like the Langebaanweg specimen because they represent species which are more primitive than that from Florida.

A summary account of the skull characters of L45062 has been given elsewhere (Hendey 1977), but they are dealt with in more detail here.

The skull of *A. africanum* (Fig. 2) differs in certain aspects from those of all living bears. Its most striking characteristic is its massive size (Table 1), although in some dimensions it is matched, or even surpassed, by skulls of male Kodiak bears (*Ursus arctos middendorffi*), which are amongst the largest of living bears (Hendey 1977, table 1). *A. africanum* is otherwise most readily distinguished from living bears by its relatively short and broad snout, while the braincase, which is surmounted by a very high sagittal crest, appears small by comparison. The nuchal crest is also very prominent and dorsally projects well behind the occipital condyles. The zygomatic arches are very stout and strongly arched. They resemble those of the giant panda, *Ailuropoda melanoleuca*, more than any other living ursid, and, amongst extinct ursids in which the zygomata are known, they are closest to those of the Florida *Indarctos* and North American *Arctodus simus* (Kurtén 1967).

In all these respects the skull of *A. africanum* is reminiscent of that of the lion, *Panthera leo*, although the latter is far smaller, and, of course, very different in detail (Fig. 3). The resemblances between the skulls of *Agriotherium* and *P. leo* are probably due to their sharing adaptations to a carnivorous way of life.

By curious contrast, the *A. africanum* skull also resembles that of the most herbivorous of all bears, *Ailuropoda*, as well as that of *Indarctos*, another supposed herbivore (Wolff 1978). This may be an indication that the actual nature of the diet is less important than the requirement in certain Carnivora

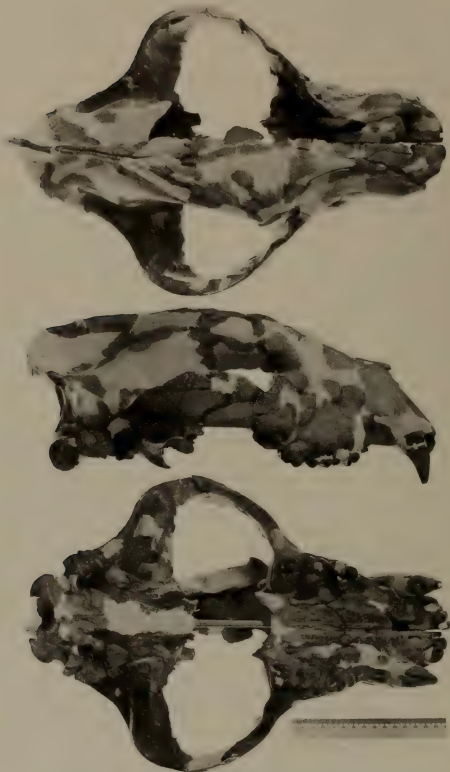


Fig. 2. Dorsal, lateral and ventral views of the Langebaanweg *Agriotherium* skull, L45062.

TABLE 1

Dimensions of Langebaanweg *Agriotherium* skull and mandible.

SKULL	L45062	L41404		
Basal length	c. 381,0	—		
Condylobasal length	c. 420,0	—		
Palate length (posterior alveolar margin of P's to posterior palatine incisure)	c. 165,0	—		
Zygomatic width	c. 305,0	—		
Rostral width (over C's)	c. 118,0	—		
Width over M's	135,0	—		
Interorbital width	c. 125,0	—		
Width over postorbital processes	c. 150,0	—		
Occiput width at base of mastoid processes	c. 130,0	—		
Condylar width	c. 90,0	—		
C-M ² length at alveolar margin	149,0	154,0		
P ¹ -M ² length at alveolar margin	83,5	82,5		
MANDIBLE	L45062	L45114	L50003	L50004
Length (C to condyle)	296,0	—	—	—
Height of ascending ramus	142,0	—	—	—
Transverse diameter of condyle	71,0	—	—	—
Depth below M ₁	69,0	68,5	c. 74,0	—
Breadth below M ₁	26,9	26,8	24,7	—
Depth at diastema	61,0	66,0	65,3	59,4
C-M ₃ length at alveolar margin	174,0	c. 190,0	c. 190,0	—
P ₄ -M ₃ length at alveolar margin	104,0	c. 117,0	111,0	—

for unusually powerful jaw musculature, with consequent similar modification of the masticatory apparatus.

There are also some similarities between the skulls of *A. africanum* and the polar bear, *Thalarctos maritimus*, which is the most carnivorous of living Ursinae. Like *A. africanum*, *Thalarctos* also has a relatively broad snout and a relatively straight dorsal profile in lateral view. These, and other, resemblances between *Thalarctos* and *A. africanum* will be discussed again later.

Although *Thalarctos* has a relatively broad snout, it is simply a modification of the 'long-faced' ursine condition, and it is easily distinguished from 'short-faced' Tremarctinae, which in turn bear a greater resemblance to *Agriotherium* and *Indarctos*, and, amongst the latter, particularly the Florida specimen.

The relatively short and broad tremarctine snouts are, however, ursine-like in having the posterior palatine incisure well posterior of the M²'s (see Kurtén 1966, 1967). By contrast, in *A. africanum* the posterior ends of the M²'s are in line with this incisure. The situation in *Indarctos* is similar (e.g. *I. atticus* from Samos—Helbing 1932; Thenius 1959), except that in this instance the M²'s project slightly more posteriorly because, unlike these teeth in *Agriotherium*, they have a talon and are more anteroposteriorly elongated. *Ailuropoda* is virtually identical to *Indarctos* in this respect. The situation of the posterior palatine incisure relative to the M²'s sets *Agriotherium*, *Indarctos* and *Ailuropoda* apart from all other later ursids.

It is worth noting here that Davis (1964: 50) believed that the lengthened palate in *Ursus* relative to that in *Ailuropoda* 'is an illusion created by the large

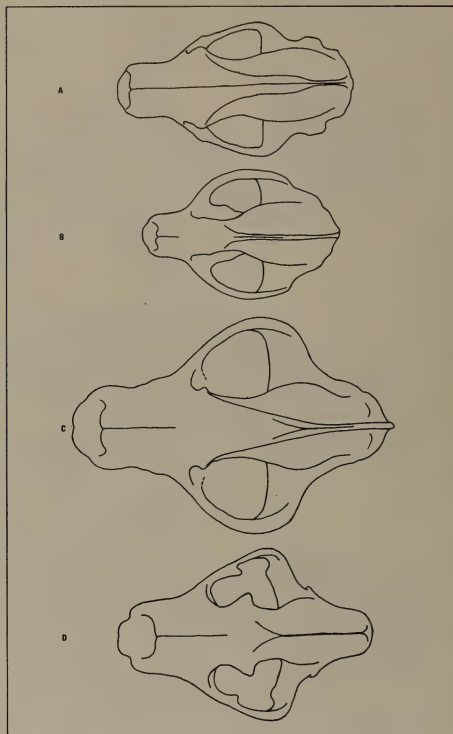


Fig. 3. Dorsal views of skulls. A. *Thalarcos*. B. *Ailuropoda*. C. The Langebaanweg *Agriotherium*. D. *Panthera leo*. A-B after Gregory (1936, figs 13-14).

teeth of the latter' and that relative 'to the anterior end of the braincase, the palate actually extends farther posteriorly in the panda.' This is true, but Davis makes no mention here of the great shortening of the posterior parts of the *Ailuropoda* skull, which undoubtedly has an effect on the position of the palate relative to the braincase.

The palate of L45062 is otherwise unremarkable, except that it lacks the minor posterior palatine foramen which is present in all other later ursids. In addition, it has a relatively small anterior median palatine foramen. In the latter respect it resembles *Indarctos* and *Ailuropoda*, and differs from the Ursinae and Tremarctinae. The minor posterior palatine foramen has apparently been incorporated with the major one, probably as a result of shortening of the palate. A vestige of the minor foramen is indicated on the posterior part of the major foramen by a shelf of bone projecting from the lateral wall of the latter. Earlier in the history of *Agriotherium* this shelf may well have extended to the medial walls of the major foramen, thus forming a separate minor foramen posteriorly.

The infraorbital foramen is situated above the posterior part of P⁴, as in *Indarctos*. This foramen is more posteriorly situated in Ursinae and some Tremarctinae, but is more anteriorly situated in *Ailuropoda*. It is relatively small compared with that in other Ursidae, and in those *A. africanum* specimens in which it is preserved (L2045, L45062, L41404) it is in the form of a single opening. In other ursids, such as the *A. sivalense* skull and some tremarctines, there may be more than one opening. The latter condition is probably of no great significance, since multiple infraorbital foramina have been observed in other carnivores (e.g. *Proteles cristatus*).

There is a marked concavity of the maxilla above the reduced anterior premolars, anteroventrally from the infraorbital foramen, which is caused by the expansion of the maxilla over the massive root of the canine and over the roots of the posterior cheek teeth. In anterior view the bulges over the canine roots completely obscure the infraorbital foramina. Amongst the Ursinae a similar tendency was observed in *Thalarctos*, although in this instance the infraorbital foramina were only partly obscured. Wolff's (1978: 2) description of the snout of the Florida *Indarctos* shows that it is essentially similar to *A. africanum*. The latter is distinct only in having features such as the bulge over the canine roots exaggerated, apparently because of the larger size of the Langebaanweg species. Wolff unfortunately provided few measurements of the Florida skull, and consequently most dimensions must be estimated from illustrations.

The nasal aperture of L45062 does not recede as markedly towards the nasals as it does in the Ursinae, and *A. africanum* resembles *Indarctos* and the Tremarctinae in this respect. This feature is evidently due to relative shortening of the snout.

Observations on the frontal region of L45062 are omitted, since there was severe fragmentation of this part of the skull and the restoration is not necessarily accurate. For example, the orbit appears smaller and the frontals more

inflated than in the skull of *A. sivalense*, in which this region is well preserved and therefore certainly accurate. It is nevertheless clear that the post-orbital processes of *A. africanum* are relatively less prominent than those of Ursinae, and the former is probably more like *Indarctos* (*I. atticus*) and *Ailuropoda* in this respect.

In his description of the zygomatic arches of *Ailuropoda*, Davis (1964: 47) stated that in dorsal view they 'form nearly a perfect circle, compared with the triangular outline in *Ursus* and other carnivores'. In *A. africanum*, which has exceedingly stout zygomata, their shape approaches that in *Ailuropoda*. The glenoid fossa and postglenoid process are also large, and in the postglenoid region a wide shelf of bone extends over the external auditory meatus, linking the zygomatic arch with the nuchal crest. The situation in *Indarctos* and *Ailuropoda* is similar, although in the latter the shelf of bone is much shorter, owing to the anteroposterior compression of the basicranial region in *Ailuropoda*. The shelf of bone is less well developed in the Ursinae.

Amongst fossil specimens the zygomata which most closely resemble those of L45062 belong to the Florida *Indarctos*, and once again Wolff's (1978: 2) description also applies to the Langebaanweg skull. The latter differs in apparently having zygomata of larger size, and in being more strongly arched and thus more *Ailuropoda*-like.

The sagittal crest of L45062 is extremely well developed, reaching a height of at least 50 mm, and, as in the Florida *Indarctos* (Wolff 1978: 2, 3), it has 'a very conspicuous cleft between the parietals'. It is, however, slightly deeper (up to 7 mm) and possibly longer (at least 70 mm) than that of the Florida skull. A similar cleft is found in the sagittal crest of *Ailuropoda* (Davis 1964).

According to Wolff (1978: 3), 'several large, rather irregularly sized and positioned nutrient foramina appear on either side of the parietals just above the temporal shelves near the posterior of the skull in several agriotheriine specimens', including the skull described by him. There are two such foramina in L41404, one on either side of the sagittal crest, immediately adjacent to it and close to its posterior limit. The same applies to L45062, but since this region of the skull is incomplete, it is possible that there were more than two such foramina.

The large size of the zygomata and enormous sagittal crest, together with various rugosities for muscle attachments similar to those of the Florida *Indarctos* (Wolff 1978), indicate that the masticatory musculature of *A. africanum* was exceptionally powerful, and in keeping with the massive canines and posterior cheek teeth of this species.

The basicranial regions of L45062, L41404, and L45137 are unfortunately poorly preserved and incomplete, although sufficient remains to show that they are ursid-like. Amongst the living Ursidae there are similarities to both Ursinae and *Ailuropoda*, while of described fossil specimens they closely resemble, and in several respects are indistinguishable from, the Samos *I. atticus* (Thenius 1949, 1959) and the Florida *Indarctos* (Wolff 1978).

As in *Ailuropoda* and *Indarctos*, the foramen rotundum and orbital fissure form a single opening in both L45062 and L41404. There is a well-developed horizontal division separating them a short distance posterior to the common opening as in the Florida *Indarctos*. In this respect *Ailuropoda* differs in that there is at most 'a paper-thin partition separating them' (Davis 1964: 49).

A. africanum is also like *Ailuropoda* and *Indarctos*, and different from most, if not all other Ursidae, in lacking an alisphenoid canal. In addition, *A. africanum*, *Indarctos*, and *Ailuropoda* are similar in that the medial edge of the glenoid fossa is closer to the foramen rotundum than is the case in the Ursinae, evidently because of the greater transverse length of this fossa in these three taxa.

The same applies in the case of the foramen ovale, which is preserved in L45062, L41404, and L45137. This foramen opens opposite the posterior wall of the glenoid fossa in these specimens, and they are similar to the Samos *I. atticus*, and probably also the Florida *Indarctos*, in this respect. In the Ursinae the foramen ovale is more posteriorly situated, while in *Ailuropoda* it is further forward.

The postglenoid foramen in *A. africanum* is situated between the external auditory meatus and the medial edge of the postglenoid process, but is closer to the latter than is the case with living ursids. Amongst the latter, *Ailuropoda* is the most distinct, since the postglenoid foramen is 'more laterally situated than in *Ursus*' (Davis 1964: 52). The situation in the Florida *Indarctos* and *I. atticus* is similar to that in *A. africanum*, although the specimen described by Thenius (1949) differs in having a double opening.

The external auditory meatus is incomplete in L45062, but it is evidently similar in position and orientation to that in the Florida *Indarctos*.

The anterior (squamosal) part of the mastoid process of L41404 is complete. It had not yet fused to the posterior (periotic) portion of this process, nor to the bone which caps this process. In size and orientation it is apparently similar to the mastoid process of the Florida *Indarctos*, and appears to have been more laterally directed than that of later ursids. Both the mastoid and paroccipital processes of L45062 are lost. The relative position of the bases of these processes differs from that in later ursids in that the base of the mastoid process is only slightly more laterally situated than that of the paroccipital process. The mastoid process of L45062 apparently differed from that of L41404 in being orientated ventrally.

Part of the lateral walls of the stylomastoid foramina, and the posterior margins of the posterior lacerate foramina, are preserved in L45062. Their positions relative to one another are as in the Ursinae and *Indarctos*. The same applies to the hypoglossal foramina and the anterior lacerate foramina.

Little of the bulla of L45062 remains. The posterior parts appear to have been more inflated than in *Ursus arctos*, and in this respect the bulla may have been more *Indarctos*-like. In overall size the bullae of *A. africanum* and a European *U. arctos* (ZM39056) were apparently similar, which is surprising in

view of the very much larger size of the *A. africanum* skull. In this respect *A. africanum* is also *Indarctos*-like. *Ailuropoda* is remarkable in that 'externally there is no indication of a bulla' (Davis 1964: 319, 320).

This is but one of the peculiarities of the *Ailuropoda* skull, which has been 'profoundly modified by the demands of mastication' (Davis 1964: 46). In less specialized ancestral forms the basicranial and other regions of the skull may well have resembled their counterparts in *Indarctos* and *Agriotherium* more closely than those in the Ursinae. The absence of the alisphenoid canal in *Indarctos*, *Agriotherium*, and *Ailuropoda* is probably the single most important basicranial character which distinguishes them from the Ursinae. This canal is present in the Canidae and all other Ursidae (Wolff 1978), including the Amphicyoninae (Ginsburg 1977; Hunt 1977) and, presumably, the Hemicyoninae.

The occipital region of *A. africanum* is known from L45062 (ventral parts) and L41404 (dorsal part and ventral part adjacent to, and including, the squamosal part of the mastoid process). In posterior view it is relatively narrow and steeply arched, rather like that of *U. arctos* and *Indarctos*. In L41404, which represents a young adult with some sutures unfused, there is an indication of a constriction above the mastoid process. In L45062, an older individual, the nuchal crest is strongly developed, and instead of passing ventrally directly on to the lateral side of the mastoid process, as in most living ursids, it is linked anteriorly with the shelf of bone which projects posteriorly from the zygomatic arch. The base of the mastoid process in L45062 is actually recessed beneath this shelf of bone. In most of the available ursine comparative specimens, the nuchal crest merges ventrally into a ridge of bone on the mastoid process, which is more laterally situated than the shelf extending posteriorly from the zygomatic arch. Only in *Thalarctos* does the arrangement approach that in *A. africanum*. It is not clear from illustrations of *I. atticus* (Thenius 1959) and the Florida *Indarctos* (Wolff 1978) which arrangement characterizes this genus.

The mandible is massive, its size being in keeping with that of the skull (Figs 4-5). It is similar in shape to that of *I. atticus* and *U. arctos*, and is distinguished principally by the presence of a premasseteric fossa. This fossa is deep in older individuals (e.g. L45062), but much less pronounced in immature adults (e.g. L45114) (Fig. 33). The only living bear with a premasseteric fossa is the South American spectacled bear, *Tremarctos ornatus*, while it is otherwise known amongst Ursidae in extinct Tremarctinae, Hemicyoninae and other species of *Agriotherium*. In tremarctines the masseteric and premasseteric fossae are separated by a prominent ridge of bone, and the latter fossa is deep, extensive and more or less circular in shape, with its limits clearly defined (e.g. see Kurtén 1966, plates 8-9). In hemicyonines the ridge separating the two fossae is not as prominent, the premasseteric fossa is less extensive in a vertical sense, but more elongated anteroposteriorly, with the anterior end gradually merging with the buccal surface of the mandible beneath M_1 (e.g. see Frick 1926, figs 2-3, 12).



Fig. 4. Buccal and dorsal views of Langebaanweg *Agriotherium* hemimandible, L45062.

The premasseteric fossa in *Agriotherium* is closer to the hemicyonine type, and may even be virtually indistinguishable from it (e.g. the *A. insigne* specimen figured by Viret (1939, fig. 6)). There are, however, *Agriotherium* specimens in which this fossa does not extend as far anteriorly, terminating instead beneath M_2 (e.g. the *A. schneideri* specimen figured by Frick (1926, fig. 36)). There is at least one specimen assigned to *Agriotherium* in which this fossa is absent (i.e. the *A. palaeindicum* specimen, GSI-D8, discussed by Pilgrim (1932)). The latter is, however, one of the problematical intermediates between *Indarctos* and *Agriotherium*, which will be discussed in a later section of this report.

The premasseteric fossae in *A. africanum* specimens are generally similar

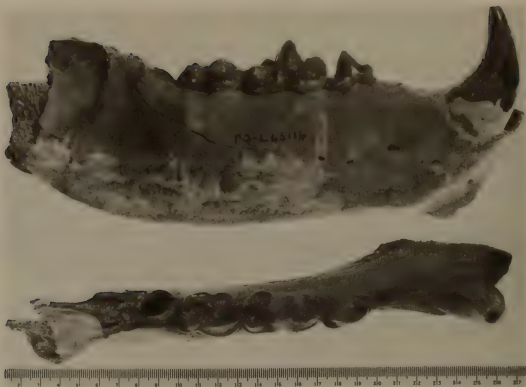


Fig. 5. Buccal and dorsal views of Langebaanweg *Agriotherium* hemimandible, L45114.

to that in the *A. schneideri* specimen mentioned above. In the four hemimandibles belonging to three individuals in which the entire premasseteric fossa is preserved, the anterior termination is beneath M_2 . These specimens apparently differ from hemicyonines and other *Agriotherium* in having a less distinct ridge of bone separating the masseteric and premasseteric fossae.

The mandible of *A. africanum* is otherwise distinguished only by the presence of a distinct 'chin' in the symphyseal region, which contrasts with the receding jaw-line in other ursids. The 'chin' is formed by an anteroventral expansion of the symphysis, which enlarges the area of the symphysis and presumably strengthened the connection between the two halves of the mandible.

With the exception of the nondescript and relatively unimportant P^1 , P^1 , P_2^2 and P_3 , all the teeth of *A. africanum* are known from at least one complete specimen still in position in a jaw. An incomplete P^1 is represented in L45062, while P^1 and P_2^2 are tentatively identified on the basis of isolated specimens. Only P_2 and P_3 have not been identified, although they could be represented amongst the six unidentified anterior premolars available. The best represented of the teeth are the larger posterior cheek teeth ($P_4^4-M_2^2$), which are, fortunately, the most informative in the dentition of *Agriotherium* (Figs 2, 6-7; Tables 2-3). These teeth are represented by between six and ten specimens belonging to between four and seven individuals.

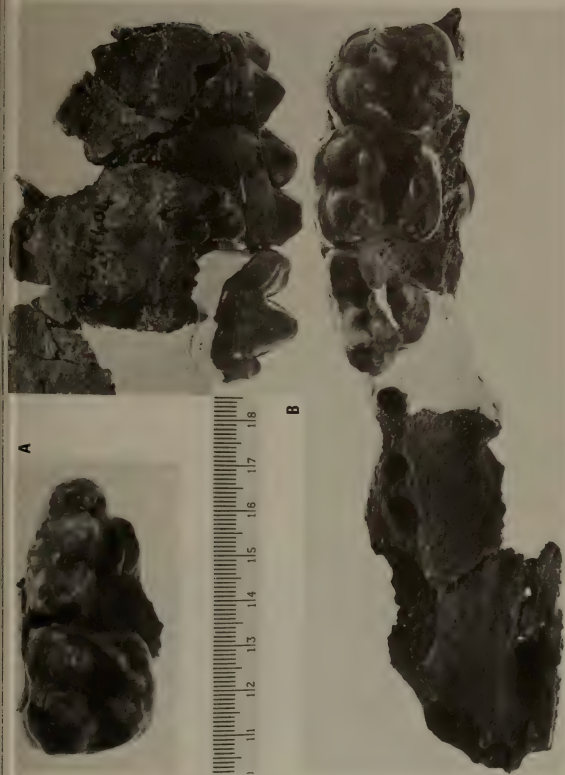


Fig. 6. A. Ventral view of Langebaanweg *Agriotherium* maxillary fragment, L55012. B. Buccal and ventral views of snout fragment, L41404.

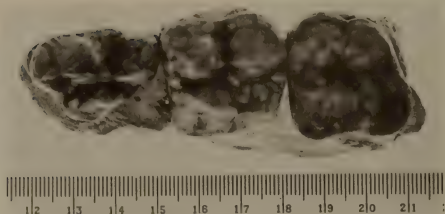


Fig. 7. Ventral view of Langebaanweg *Agriotherium* maxillary fragment, L45137.

Apart from their large size, the incisors of *A. africanum* are unremarkable and are little different from those of living Ursinae. Dimensions of some incisors were given elsewhere (Hendey 1977, tables 2, 5). The I^2 is distinct in having two lingual cusps projecting from the V-shaped cingulum posterior to the principal (spatulate) cusp. The lateral accessory cusp is the smaller and the more anteriorly situated, being little more than a small projection from the cingulum. The other accessory cusp is much larger, covering much of the lower part of the lingual surface, although it is still much smaller than the principal cusp (Fig. 8). In older individuals (e.g. L45062) the three cusps develop horizontal wear facets in a single plane. The I^1 is similar to I^2 , but smaller, while the I^3 , which is the largest of the incisors, is morphologically similar to its counterpart in Ursinae.

The lower incisors are similar to those of *Ursus arctos* and other ursines, and are distinguished only by their larger size.



Fig. 8. Medial, posterior and lateral views of Langebaanweg *Agriotherium* I^2 , unnumbered Dump 8 specimen.

TABLE 2
Dimensions of Langebaanweg *Agriotherium* upper teeth.

NUMBER	HORIZON	L/R	C		P ³		P ⁴		M ¹		M ²	
			l	b	l	b	l	b	l	ab	l	ab
L2045	. . bed 3aS	L	—	—	—	—	c. 32,8	25,5	—	—	—	—
L45062	. . bed 3aN	L	27,0	c. 21,0	9,5	7,5	32,6	24,3	28,1	30,0	26,4	29,9 c. 27,8
		R	27,8	21,2	9,7	7,6	31,9	c. 24,5	28,5	29,5	26,5	30,2 27,3
L45137	. . bed 3aN	L	29,2	20,6	—	—	31,6	22,0	30,3	29,1	c. 29,3	31,5 29,1
		R	c. 29,2	c. 21,6	—	—	31,2	22,7	29,8	28,9	29,2	31,4 29,3
L41404	. . bed 3aN	L	—	—	—	—	32,5	24,2	28,5	30,9	26,5	31,0 28,5
L55012	. . bed 3aN	L	—	—	—	—	33,0	24,4	—	—	—	—
		R	—	—	—	—	33,0	25,0	29,2	28,6	30,1	—
L46074	. . bed 3aN	R	—	—	—	—	33,3	24,1	—	—	—	—
L50008	. . bed 3aN	R	—	—	—	—	35,8	c. 25,0	—	—	—	—
L48564	. . bed 3aN	L	—	—	—	—	—	—	—	—	25,6	30,5 29,5
L48577	. .	R	—	—	—	—	—	—	—	—	25,4	30,2 27,7
L47242	. . bed 3aN	R	—	—	—	—	—	—	—	—	25,8	25,9 23,9
L47698	. . bed 3aN	L	—	—	—	—	—	—	—	—	31,1	30,1 28,6
Means	28,3	21,1	—	—	32,8	24,2	29,1	29,5	27,5	30,1 28,0
Ranges	27,0– 29,2	20,6– 21,6	—	—	31,2– 35,8	22,0– 25,5	28,1– 30,3	28,6– 30,9	25,4– 31,1	25,9– 31,5 23,9– 29,5
n	4	4	—	—	10	10	6	6	9	9 9 9

L = Left ; R = Right

TABLE 3

Dimensions of Langebaanweg *Agriotherium* lower teeth.

NUMBER	HORIZON	L/R	\bar{C}		P_1		P_4		M_1			M_2		M_3	
			l	b	l	b	l	b	l	ab	pb	l	b	l	b
L12561 .	bed 3aS	R	—	—	—	—	—	—	—	—	—	—	—	16,5	16,7
L45062 .	bed 3aN	L	29,8	19,8	12,8	8,1	21,8	14,2	39,7	20,3	23,0	29,3	24,0	16,2	16,6
		R	c. 29,0	—	12,8	8,3	c. 22,4	14,0	39,7	19,7	22,3	28,6	c. 23,6	17,1	17,0
L46563 .	bed 3aN	L	—	—	—	—	—	—	—	—	—	33,5	24,3	—	—
L45114 .		R	33,8	21,7	—	—	25,4	15,5	43,1	20,7	22,8	32,6	23,5	—	—
L50003 .	bed 3aN	L	—	—	—	—	24,5	15,5	—	—	—	30,4	24,1	—	—
L50004 .	bed 3aN	L	—	—	—	—	24,0	16,8	43,4	22,1	24,8	32,3	26,0	—	—
L50445 .	bed 3aN	L	—	—	—	—	23,5	15,0	—	—	—	—	—	—	—
L50446 .	bed 3aN	R	—	—	—	—	—	—	44,0	19,8	23,4	—	—	—	—
L50005 .	bed 3aN	R	—	—	—	—	—	—	43,9	20,2	22,9	—	—	—	—
L50006 .	bed 3aN	L	—	—	—	—	—	—	37,8	18,5	21,1	—	—	—	—
L50007 .	bed 3aN	R	—	—	—	—	—	—	—	—	—	28,8	21,9	—	—
L50981 .	bed 3aN	L	—	—	—	—	—	—	—	—	—	—	—	19,8	19,0
Means	30,9	20,8	—	—	23,6	15,2	41,7	20,2	22,9	30,8	23,9	17,4	17,3
Ranges	c. 29,0– 33,8	19,8– 21,7	—	—	21,8– 25,4	14,0– 16,8	37,8– 44,0	18,5– 22,1	21,1– 24,8	28,6– 33,5	21,9– 26,0	16,2– 19,8	16,6– 19,0
n	3	2	—	—	6	6	7	7	7	7	7	4	4

L = Left ; R = Right

The canines are similarly remarkable only for their large size. Otherwise they differ from the canines of Ursinae only in being less elongated anteroposteriorly.

All the known anterior premolars (P_1^1 to P_3^3) are small, low-crowned and single-rooted teeth. The P_1 is slightly elongated anteroposteriorly, and the crown is divided longitudinally by a crest in the enamel. This is evidently the remnants of the anterior and posterior keels which have merged into a single feature as a result of reduction of the principal cusp, and its disappearance as an identifiable element in this tooth. The enamel on the buccal side of the crest is smooth, while that on the lingual side is slightly rugose. The P^3 is similar, but is more circular in outline, while the crest is convex buccally, with vestiges of the principal cusp still evident. The tentatively identified P^1 (L55017A) fits the P^1 alveolus of L45062 well and may even belong to this specimen. It is similar to P_1 , but is slightly broader posteriorly, and with vestiges of the principal cusp still evident.

The P_4 of *A. africanum* is much larger than the anterior premolars, and in relative size and morphology it is not unlike its counterpart in the Ursinae. It is a stout, double-rooted tooth, with a prominent principal cusp, and in lateral view the anterior and posterior halves are almost mirror images of one another. The tooth is broader posteriorly due to the presence of a postero-lingual bulge in the cingular region. The anterior and posterior keels of the principal cusp are well defined but rather blunt, and terminate ventrally on cusplless horizontal shelves. The posterior shelf is fringed by a well-developed cingulum. Much of the P_4 enamel is finely rugose, which is also the case in other posterior cheek teeth of *A. africanum*. The apex of the principal cusp develops a horizontal wear facet, which merges with an inclined facet on the posterior keel.

The P^4 of *A. africanum* (Fig. 9) is an important tooth, since it was largely on its characteristics that the species was identified (Hendey 1972). The P^4 of the holotype (L2045) has been exhaustively described (Hendey 1972; Wolff *et al.* 1973), while examples from the bed 3aN sample have been briefly discussed (Hendey 1977). The P^4 of L2045 is unlike that of any previously described *Agriotherium* because of the presence of a large accessory cusp antero-internally, that is, the anterior end of the protocone lobe. It is now evident that this feature also distinguishes it from the P^4 's of the bed 3aN sample, in which this cusp may be present but small (e.g. L45137), or very small (e.g. L45062), although it may also be absent (e.g. L41404). The P^4 of the *A. africanum* holotype is thus atypical of the species sample as a whole. It is, however, not necessarily an abnormal specimen, but may well be a typical example from a population which predates, and is therefore more primitive than that represented in bed 3aN.

The bed 3aN P^4 sample, which is comprised of nine specimens belonging to six individuals, includes only one in which the antero-internal cusp is absent (i.e. L41404). Consequently, this cusp can still be regarded as a characteristic of the species. A similar situation does, however, exist in respect of the *A. insigne*



Fig. 9. Buccal, occlusal and lingual views of Langebaanweg *Agriotherium* P⁴'s.
A. L46074, from bed 3aN. B. L2045, from bed 3aS.

from Montpellier in France. A specimen described by Gervais (1859) apparently lacks an antero-internal cusp, but an undescribed specimen from the same locality (NMB-MP549) has a large antero-internal cusp on its P⁴. For this, and other reasons, *A. africanum* should perhaps be regarded as a junior synonym of *A. insigne*, a matter which will be pursued in a later section of this report.

There is apparently one feature of P⁴ in which *A. africanum* may be unique. In L2045 there is a small wear facet situated between the antero-internal cusp and the apex of the protocone, which was interpreted as the vestiges of another accessory cusp on the protocone lobe by Hendey (1972). Wolff *et al.* (1973) dismissed this interpretation, and regarded this feature simply as a wear facet caused by occlusion with M₁. It is undoubtedly such occlusion which caused the wear facet, but Wolff and his co-authors overlooked the fact that it is impossible to get dentine exposed at the same level as enamel unless there had previously been a small cusp in this position. The difference of opinion is conclusively resolved by the fact that the bed 3aN sample includes unworn examples of this accessory 'intermediate' cusp. It has already been recorded elsewhere (Hendey 1977: 114) that the P⁴ of L41404, although lacking an antero-internal cusp, does have 'a small, more posteriorly situated cusp which apparently corresponds to the "intermediate cusp" of the holotype'. Another specimen is now known (L46074) in which both an antero-internal cusp and an 'intermediate cusp' are present and unworn. As with the antero-internal cusp, the 'intermediate cusp' of L2045 must have been more prominent than that of any bed 3aN specimen.

The buccal cusps of the *A. africanum* P⁴ are unremarkable. All ten specimens have prominent parastyles, which is characteristic of the genus and of some advanced *Indarctos* specimens (see p. 81). The P⁴ has three roots, two beneath the buccal cusps and one beneath the lingual ones. The M¹ and M² of *A. africanum* are similar in this respect, although the lingual root is larger in these teeth.

The wear facets on P⁴ were discussed by Hendey (1972) and Wolff *et al.* (1973), and the only additional observation possible is that the parastyle develops a crescentic facet which is inclined anterolingually.

The seven M₁'s belonging to four *A. africanum* individuals are, in general, similar to those of previously described *Agriotherium* (Fig. 10A). The trigonid makes up the bulk of the tooth, with the protoconid being particularly large and prominent. Although the shearing facets normally found in carnivore lower carnassials are evident on the buccal surfaces of the paraconid and protoconid, the apices of these cusps also develop horizontal facets. In addition, the single anterior, and two divergent posterior keels of the protoconid may be obliterated by inclined facets. Cingula are developed on both sides of the paraconid, with that on the lingual side being more pronounced. There are usually only two talonid cusps clearly developed, a prominent, rather bulbous one on the lingual side, and a low, ridge-like one on the buccal side. The latter develops a horizontal wear facet, while the large lingual cusp develops a posterobuccally

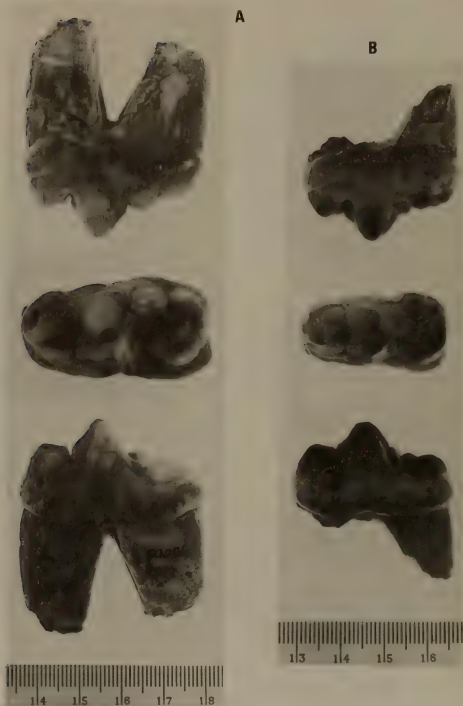


Fig. 10. Lingual, occlusal and buccal views of Langebaanweg *Agriotherium* M₁'s. A. L50004, a male specimen of typical morphology. B. L50006, a female specimen with vestigial ?metaconid.

inclined facet. There is a ridge of enamel posterior to this cusp which may take the form of a low cusp, as in L50004.

There are two M_1 's in the assemblage which deviate from the basic cusp pattern described above. An isolated specimen, L50006, which is the smallest of the M_1 's, and which evidently belonged to a female, has a small additional cusp situated between the protoconid and the large lingual talonid cusp (Fig. 10B). This specimen is also unusual in having only a lingual posterior keel on the protoconid, the buccal one, which is usually less pronounced, being absent. In addition, the ridge anterior to the buccal talonid cusp is directed towards the additional cusp, rather than directly anteriorly as is usually the case. The second unusual M_1 is L50446, which is distinct in having two small cusps situated posterior to the large lingual talonid cusp. The possible significance of these specimens will be discussed later (see pp. 83, 84).

Both M_1 and M_2 have two roots, a larger one supporting the trigonid and the other supporting the talonid.

The M^1 of *Agriotherium* has the basic four-cusped pattern typical of all later ursids, and this tooth of *A. africanum* is little or no different from its counterparts in previously described *Agriotherium*. The paracone and metacone are prominent conical cusps of similar size, which develop horizontal wear facets on their apices, and inclined facets posterolingually. The protocone is a ridge-like cusp directed anterobuccally at a slight angle to the anteroposterior axis of the tooth. The hypocone is conical and less voluminous than the protocone. The two lingual cusps are lower crowned than the buccal ones. There are lingual and buccal cingula which are distinct largely because the enamel is smooth, whereas that elsewhere tends to be rugose. The cingular region bulges anterolingually, and this results in the length of the tooth measured over the lingual cusps being close to the buccal (maximum) length. In addition, the breadth measured over the two anterior cusps is comparable to the posterior breadth measurement, and to the two length measurements. In other words, the M^1 of *A. africanum* is more or less square in outline. *Agriotherium* is unique amongst later ursids in this respect. In the Ursinae, Tremarctinae, *Indarctos* and *Ursavus* the M^1 's are rectangular with lengths exceeding breadths, while in *Ailuropoda* the situation is reversed and the M^1 is broader than it is long.

The M_2 of *A. africanum* also has a basic four-cusped pattern, but in this instance the two largest cusps (paraconid and protoconid) are situated anteriorly, rather than buccally as in M^1 (Fig. 11A). There are, however, three teeth belonging to at least two individuals which deviate from this pattern. They are L45115 and L46563 (Figs. 5, 11B) which probably belong to one individual, and L50007, which belongs to a smaller individual, probably a female. In these specimens the anterolingual cusp is reduced or absent. Reduction is evident in L50007 where the anterolingual cusp is situated closer to the anterobuccal cusp, with its anterior and posterior keels directed accordingly. This gives the impression that it is merging with the anterobuccal cusp, rather than simply reducing in its usual position. In L45114/L46563 the anterolingual

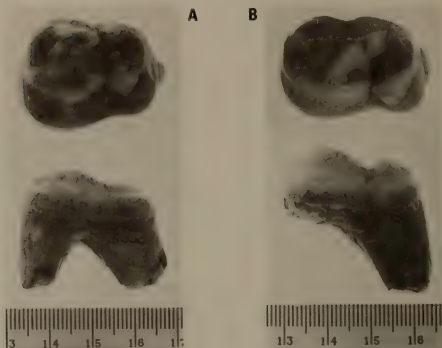


Fig. 11. Occlusal and buccal views of Langebaanweg *Agriotherium* M_2 's. A. L50004, a specimen of typical morphology. B. L46563, a specimen lacking the anterolingual cusp.

cuspid is absent, and its posterior keel is linked to the apex of the anterobuccal cusp. Only vestiges of the anterior keel remain. These three teeth are also distinct in being relatively narrower than others in the M_2 sample. The M_2 cusps develop horizontal wear facets, while there are also inclined facets antero-buccally and on the buccal surface of the posterobuccal cusp.

The M^2 of *A. africanum*, like the P^4 , is an important tooth, and it is fortunately well represented (Fig. 12). It is essentially similar to M^1 in its basic cusp

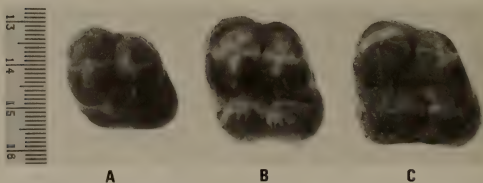


Fig. 12. Occlusal views of Langebaanweg *Agriotherium* M^2 's. A. L47242 (reversed). B. L48564. C. L47698.

morphology. The paracone and metacone are the most prominent of the four cusps, although in this instance the metacone is a little smaller than the paracone. The protocone is ridge-like, while the hypocone is more conical, although it tends to be less distinctly developed than the other cusps. There is an expansion of the lingual cingulum adjacent to the protocone, and sometimes also in the posterolingual part of the tooth. The latter expansion is significant since it represents the vestiges of the talon which was present in ancestors of *Agriotherium* (see page 87). As with the other molars, the cusps develop horizontal wear facets, while there are also inclined facets developed anterolingually on the paracone and metacone.

The M_3 of *A. africanum* is a relatively simple, single-rooted tooth, which tends to be circular in occlusal view, with no distinct cusps developed (Fig. 13).

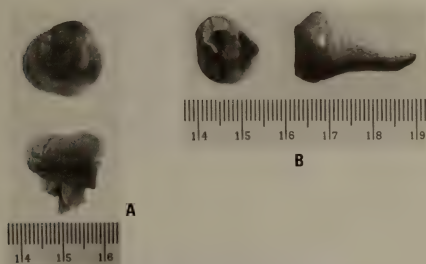


Fig. 13. A. Occlusal and lingual views of Langebaanweg *Agriotherium* M_3 , L50981.
B. Occlusal and posterior views of M_3 , L12561.

The occlusal surface is in the form of a shallow basin surrounded by a low ridge of enamel. This ridge develops a horizontal wear facet, and the entire occlusal surface would presumably be worn flat in older individuals. There is also an inclined wear facet anterobuccally. This region of the tooth tends to be slightly expanded, which emphasizes a posterior tapering which is best seen in the specimen L50981.

More detailed comparisons between the teeth of *A. africanum* and other taxa will be made in a later section of this report.

THE POSTCRANIAL SKELETON

The present study of *A. africanum* postcranial bones has been superficial, largely because adequate modern comparative material was not available and

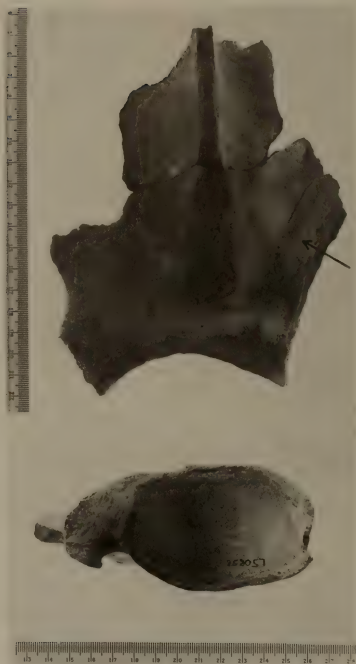


Fig. 14. Lateral and ventral views of Langebaanweg *Agriotherium* scapula, L50858. Arrow indicates postscapular fossa.

because of the lack of direct access to relevant fossil material. Little has hitherto been published on the postcranial skeleton of *Agriotherium* and other late Tertiary ursids, and although meaningful interpretation of the evolutionary and functional significance of *A. africanum* bones is no doubt possible, the following account of them is essentially descriptive. In this account references are made to bones of a male European *Ursus arctos* (ZM39056), a male Asian *Euarctos* (ZM38805) and a female *Helarctos* (ZM36289), all of which are zoo specimens. Reference is also made to the limb bones of *Ailuropoda* as described by Davis (1964).

In general, the bones of *A. africanum* are larger and more stoutly proportioned than those of the *U. arctos* comparative specimen, but they are essentially similar morphologically.

The available vertebrae of *A. africanum* are all incomplete, and most are very fragmentary. Except for their larger size, they are similar to those of the available comparative specimens and *Ailuropoda*. No ribs definitely identified with *A. africanum* are known.

The only identified *A. africanum* scapulae, L50857/8, may belong to one individual, although L50858 differs in showing indications of mild osteoarthritis (Fig. 14). Both specimens lack most of the blades. The glenoid fossa is anteroposteriorly elongated and tapers anteriorly, much like those in the ursine comparative specimens and the *Ailuropoda* specimen illustrated by Davis (1964, fig. 46). The preserved parts of the blades of *A. africanum* scapulae are also similar to those of ursines and *Ailuropoda*, except for one marked difference which may be of great functional significance.

Davis (1964: 91) has recorded that there are differences in the nature of the postscapular fossae in *Ailuropoda* and *U. arctos*, and, judging from the available comparative specimens, there is appreciable variation of this fossa in Ursinae. It is only the lower parts of this fossa which can be observed in L50857/8, and these specimens are distinct in having the inferior scapula spine terminating on the lateral surface of the blade 50 to 60 mm above the glenoid fossa, instead of terminating posteriorly at the glenoid fossa. Consequently, the postscapular fossa in *A. africanum* is confined to the lateral surface of the scapula, whereas the lower part of this fossa is on the medial surface in *Ailuropoda*, *U. arctos* and *Helarctos*, and posteromedially in Asian *Euarctos*.

According to Davis (1964: 91, 173) the postscapular fossa 'lodges the subscapularis minor muscle' which is the main 'medial rotator of the arm'. The functional significance of its distinct orientation in *A. africanum* is not known.

No complete humerii of *A. africanum* are preserved, the best available specimen being L45063, in which the proximal end is detached and slightly crushed, and part of the proximal part of the shaft is lost (Fig. 15, Table 4). The humerus is otherwise known from several fragmentary specimens, mainly distal ends. All the important features of the humerus, except overall length, can be observed. It is one of the many *A. africanum* bones in which available speci-



Fig. 15. Posterior, lateral and anterior views of Langebaanweg *Agriotherium* humerus, L45063.

mens exhibit appreciable size variation, larger specimens presumably belonging to males and smaller ones to females. The latter include L45063.

In its basic morphology the humerus of *A. africanum* is similar to those of Ursinae. Proximally it is similar to corresponding parts of ursine humeri in all observable respects, but distally there are some differences, although like the Ursinae, and unlike Tremarctinae and *Ailuropoda*, it lacks the entepicondylar foramen. However, vestiges of the bar of bone enclosing this foramen, in the

TABLE 4
Dimensions of Langebaanweg *Agriotherium* humerii.

	L40040	L45063
Max. ant.-post. diam., distal end . . .	91,7	67,0
Max. transv. diam., distal end . . .	121,5	98,5
Max. transv. diam., distal articulation .	92,7	76,4

form of a rugosity at its proximal termination, are more obvious in *A. africanum* than Ursinae.

The olecranon fossa is deep and relatively narrower than its counterparts in available ursine humerii, although it is closer to the Ursinae than *Ailuropoda* in this respect (see Davis 1964: 95, fig. 49). There is a relatively greater antero-posterior development of the *A. africanum* humerus distally, although once again it is closer to Ursinae than *Ailuropoda*. The medial epicondyle is much less prominent than in ursines, although the lateral epicondyle is similarly developed.

The lateral epicondylar ridge is more constricted above the lateral epicondyle than in ursines. This ridge has a relatively greater length than those of *U. arctos* and *Helarctos*, but that of Asian *Euarctos* is comparable in this respect. This is a reflection of the relatively greater elongation of the humerii in *A. africanum* and *Euarctos*.

The proximal termination of the lateral epicondylar ridge is more or less opposite the point of convergence of the deltoid and pectoral ridges (the deltoid tuberosity), as in ursines. The pectoral ridge is much like that of ursines, but the deltoid ridge is more prominently developed, and proximally it is more anteriorly situated. Consequently, the area between these two ridges faces anteriorly over a greater distance than in the ursines. This is the area of insertion of the cephalohumeral muscle, which is the chief extensor of the foreleg (Davis 1964: 95, 167). The functional significance of the more anterior insertion, and apparently greater development of this muscle, is not known.

Some of the characteristics of the ulna of *A. africanum* have already been discussed elsewhere (Wolff *et al.* 1973), but more and better specimens are now available (Fig. 16, Table 5). Once again the most complete specimen is L45063, which belongs to a smaller individual than the previously described specimen (L2154). Apart from the size difference, these two specimens are similar in all observable respects. The *A. africanum* ulna resembles those of available ursine specimens, and other ursids, including the *Indarctos atticus* specimen from Samos described by Pilgrim (1931). The proportions of L45063 are similar to those of the *U. arctos* comparative specimen.

In lateral view the *A. africanum* olecranon does not project as markedly as in ursines, and its medial tapering is usually less pronounced. The olecranon is, however, very broad transversely. The area for insertion of the triceps and flexor carpi ulnaris muscles is therefore large, although that for the insertion of the latter is less knob-like. In the Ursinae and *Ailuropoda* the area for insertion of the most proximal part of the anconeus muscle is prominently developed (see



Fig. 16. A. Medial view of Langebaanweg *Agriotherium* ulna, L46076. B. Anterior and lateral views of ulna, L45063.

TABLE 5
Dimensions of Langebaanweg *Agriotherium* ulnae.

	L50763	L50805	L50808	L40044	L12383	L46076	L45062(R)	L2154	L45063
Overall length	—	—	—	—	—	—	—	—	416,0
Transv. diam. of anconeal process	28,0	—	—	—	27,6	26,5	25,8	—	22,6
Transv. diam. of coronoid process at radial notch	47,0	—	—	—	41,6	42,1	40,7	38,4	38,5
Diam. of semilunar notch	45,6	—	—	—	41,5	44,0	40,7	—	39,7
Ant.-post. diam. at anconeal process	93,8	—	—	—	—	86,5	84,5	—	74,5
Ant.-post. diam. at semilunar notch	58,0	—	—	—	—	56,0	60,6	56,0	46,0
Ant.-post. diam. at coronoid process	—	—	—	—	—	87,5	94,2	—	68,8
Long diam. of styloid process	41,7	—	41,5	38,8	—	—	—	—	32,0
Short diam. of styloid process	22,6	22,2	22,2	22,2	—	—	—	—	20,0

(R) = Right

Davis 1964: fig. 50), but is less so in *A. africanum*, especially female specimens such as L45063. Once again, the functional significance of these differences is not known.

The semilunar notch differs from those of ursines and *Ailuropoda* in some respects. In lateral view it is almost perfectly semicircular, with the inner borders of the notch not divergent at their extremities as in ursines, and not showing the beginnings of convergence as in *Ailuropoda* (see Davis 1964, figs 50–51). In anterior view the dorsal part is nearly parallel-sided, rather than sharply tapering as in ursines. The anconeal process of *A. africanum* is therefore relatively broad. This, and the relatively narrow olecranon fossa of the humerus, are probably directly related features. When the humerus and ulna of *A. africanum* are articulated and fully extended the olecranon fossa is nearly completely filled by the anconeal process, and little lateral movement of the ulna is possible. In the ursines only about half the olecranon fossa is filled and appreciable lateral movement is possible. Much the same evidently applies in the case of *Ailuropoda*, which has an even wider olecranon fossa than ursines, while Davis (1964: 96) noted that there was no protection against lateral shifting of the elbow joint. The significance of these contrasting situations is not known.

The shaft of the *A. africanum* ulna is very stout, and although the areas for attachment of the brachialis tendon and interosseous ligament vary both in size and form, they are very pronounced features.

Distally the radial articular facet is relatively, and sometimes absolutely, smaller than its counterpart in ursines. Medially between this facet and the styloid process is a deep and almost circular depression, which is directly in line with the prominent ridge on the shaft separating the areas of insertion of the pronator quadratus and the distal part of the flexor digitorum profundus 5 muscles. This depression is absent in available ursine specimens, and apparently also in *Ailuropoda* (Davis 1964, fig. 50). Its significance is not known.

The radius of *A. africanum* is represented by several proximal and distal fragments, but only one that is complete (L40044), while another has been restored (L45063) (Fig. 17, Table 6). The latter belongs to a female and L40044 to a male. These two specimens differ only in size. They are typically ursid in their characteristics, the proximal end being particularly distinctive, and L40044 is very similar in its proportions to the *I. atticus* specimen described by Pilgrim (1931). The latter specimen is, however, distinct in having a broad groove on the anterior surface towards the distal end. Pilgrim (1931: 27) thought this noteworthy since 'a similar structure exists in a corresponding position in the radius referred by Falconer to *Agriotherium* . . . *sivalense*'. According to Pilgrim it is also present in *Amphicyon*, although it is evidently not characteristic of all amphicyonines (see Ginsburg 1977, fig. 25). Since the radius of *A. africanum* is otherwise unremarkable, it is not described in detail.

With one exception, all the carpal bones characteristically present in Ursidae are represented by at least one, and as many as nine, complete specimens (Fig. 18, Table 7). The exception is the radial sesamoid, which was evi-

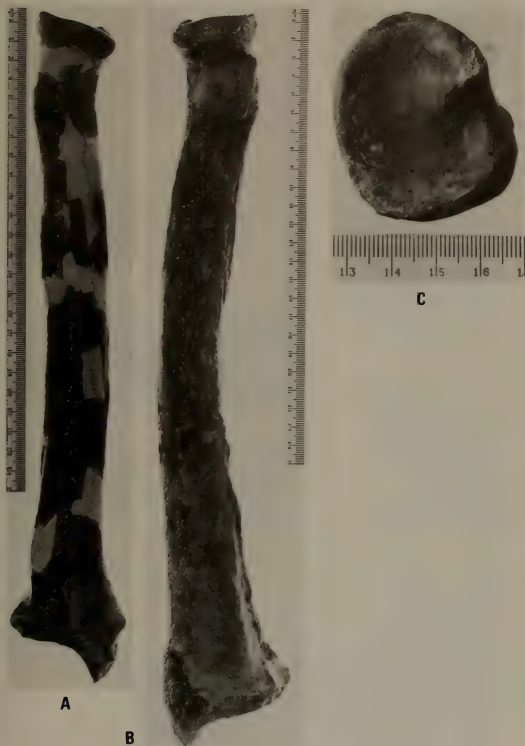


Fig. 17. A-B. Medial views of Langebaanweg *Agriotherium* radii. A. L45063. B. L40044. C. Proximal view of L40044.

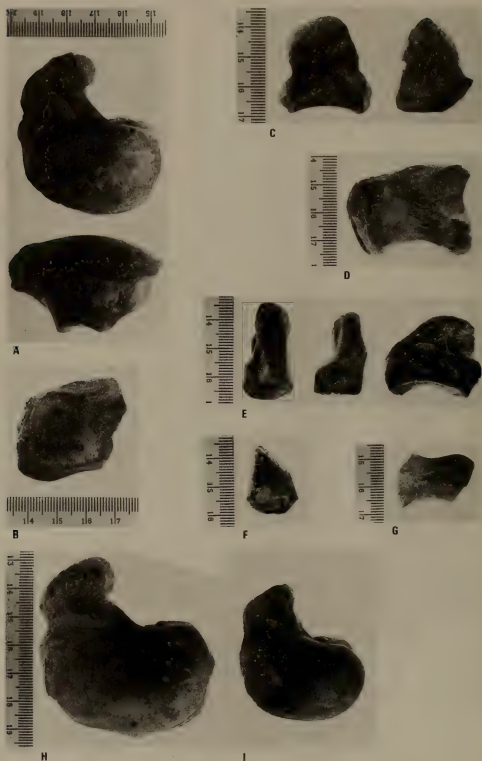


Fig. 18. Carpal bones of Langebaanweg *Agriotherium*. A-G. L45063. H. L46134. I. L50767 (reversed). A. Proximal and dorsal views of scapholunar. B. Medial view of cuneiform. C. Medial and dorsal views of unciform. D. Anterior view of pisiform. E. Proximal, dorsal and lateral views of magnum. F. Proximal view of trapezoid. G. Lateral view of trapezium. H.-I. Specimens illustrating size range of scapholunars.

TABLE 6
Dimensions of Langebaanweg *Agriotherium* radii.

	L50806	L48747	L45062	L40044	L47699	L33826	L45063	L50816	L40003
Overall length	—	—	—	404,0	—	—	345,0	—	—
Max. ant.-post. diam., proximal end	44,1	43,8	—	41,6	c. 38,5	37,8	36,5	34,7	33,7
Max. transv. diam., proximal end	56,4	56,2	52,8	50,7	c. 49,0	50,3	45,4	47,4	—
Max. ant.-post. diam., distal end	—	—	—	49,0	—	—	c. 42,5	—	—
Max. transv. diam., distal end	—	—	—	70,5	—	—	63,7	—	—

TABLE 7
Dimensions of Langebaanweg *Agriotherium* carpals.

	SCAPHOLUNARS							PISIFORMS				
	L46134	L50635	L45062	L45063	L41702	L48021	L50767		L46134	L45062	L12503	L45063
Max. ant.-post diam.	67,0	62,8	60,2	58,0	55,7	48,3	45,6	Overall length	53,8	52,2	51,0	48,4
Max. ant.-post. diam. of radial facet	38,6	38,6	38,1	34,0	33,8	30,9	29,1	Prox. long diam.	39,0	36,5	37,0	33,9
Max. transv. diam.	63,9	60,0	61,5	53,1	55,0	49,1	44,5	Prox. short diam.	26,7	22,9	20,6	19,9
Max. dorsoventral diam.	38,0	—	39,2	35,2	33,8	c. 28,5	26,5	Dist. long diam.	42,7	38,0	39,0	34,2
								Dist. short diam.	28,7	28,4	30,0	23,8
	CUNEIFORMS				MAGNUMS			UNCIFORMS				
	L50795	L45062	L45063	L50786	L50794	L33160	L50457	L47074	L45062	L45063	L50774	L50772
Max. ant.-post. diam.	48,0	44,3	38,7	—	43,3	41,6	38,9	38,7	38,5	34,5	39,1	38,0
Max. transv. diam.	42,0	36,7	32,5	31,5	24,3	22,0	20,3	21,5	20,8	17,4	36,2	33,6
Max. dorsoventral diam.	—	—	—	—	36,5	34,1	33,0	36,0	33,1	28,8	42,8	37,6
											33,5	30,4
											30,1	30,6
											33,9	34,9

dently absent in *A. africanum*, since the scapholunar lacks the radial sesamoid facet. In this respect *A. africanum* is very different from *Ailuropoda*, in which the radial sesamoid is better developed than in any other arctoid carnivore (Davis 1964: 99, 100). A small radial sesamoid is apparently usually, or always, present in Ursinae, and is larger in Tremarctinae. Otherwise the carpals of *A. africanum* are essentially similar to their counterparts in Ursinae.

The largest carpal, the scapholunar, is also the best represented. As with other *A. africanum* bones, the scapholunars exhibit appreciable size differences, the smallest (L50767) being only about two-thirds the size of the largest (L46134) (Fig. 18H-I). This is a slightly greater size difference than that observed in the scapholunars of North American *Tremarctos floridanus*, an ursid of similar overall size (Kurtén 1966, table 19), although in both instances sample sizes are small. There are no significant morphological differences between the smallest and largest scapholunars, and they differ in only minor respects from those of ursines. In the latter the cuneiform facet tends to be clearly distinct from the unciform facet, but in *A. africanum* they merge and are distinguishable only because the cuneiform facet is flattened and the unciform facet is concave. In some specimens (e.g. L48021) the proximal (radial) articular surface is in contact anteriorly with the articular facet of the trapezium, and in this respect *A. africanum* is similar to *Ailuropoda* (see Davis 1964: 99). The proximal articular surface of the *A. africanum* scapholunar is also *Ailuropoda*-like, and different from Ursinae, in lacking the lateral depression which receives 'the saddle on the distal end of the radius' (Davis 1964: 99).

The cuneiform of *A. africanum* is morphologically similar to that of *U. arctos*, except that the scapholunar facet is more elongated. In addition, this bone is relatively more flattened than that of *U. arctos*.

Such minor differences in morphology and proportions also distinguish other *A. africanum* carpals from their *U. arctos* counterparts. For example, in the *A. africanum* unciform, the magnum and scapholunar facets are not confluent as in *U. arctos*, while the pisiform is a considerably stouter bone. At least some of the distinctive features in *A. africanum* carpals may be due to the large size of the species, but their possible significance in other respects was not investigated.

Of the metacarpals of *A. africanum* only the second is not represented by a complete specimen, although there is one which lacks only the distal end (L33160). All the metacarpals are similar to their counterparts in ursines in terms of morphology, but are relatively more massive (Fig. 19, Table 8). In spite of this, they are not necessarily much longer than those of the available *U. arctos* specimen. One of the complete metacarpals I (L45448) is in fact similar in length to that of the *U. arctos* comparative specimen, although it has a much stouter proximal end and shaft. The *A. africanum* metacarpals appear to be readily distinguishable from those of *Ailuropoda*, which are 'short and stout, relatively considerably shorter than in [other bears] of comparable size' (Davis 1964: 100).



Fig. 19. Proximal, anterior and lateral or medial views of Langebaanweg *Agriotherium* metacarpals. A. I, L50775. B. III, L25862. C. IV, L33828. D. V, L45063.

TABLE 8
Dimensions of Langebaanweg *Agriotherium* metacarpals.

	I				II		III						
	L50775	L45063	L55029	L45448	L33160	L33160	L50810	L25862	L20998	L45062	L50788	L45063	L50783
	Overall length	81,2	—	81,2	76,9	—	—	121,9	113,6	—	117,5	—	117,1
	Max. ant.-post. diam., prox. end	25,3	23,0	22,7	—	24,8	36,5	—	36,2	32,6	31,8	31,3	—
	Max. transv. diam., prox. end	25,7	22,2	23,6	—	34,6	25,0	—	22,0	20,4	20,7	—	c. 20,0
Max. ant.-post. diam., dist. articulation	17,4	—	17,3	17,2	—	—	—	24,8	24,5	—	23,5	—	c. 22,5
	18,7	—	17,6	17,3	—	—	—	23,0	24,8	—	22,0	—	c. 21,7
	Max. transv. diam., dist. articulation												
	IV				L45063		V						
	L33160	L48432	L33828	L41575	L45063	L33160	L33160	L45063	L33160	L45063	L33160	L45063	L33160
	Overall length	—	126,1	120,4	117,7	—	—	106,2	—	—	—	—	—
	Max. ant.-post. diam., prox. end	37,5	36,3	34,3	—	32,3	37,0	29,9	33,5	37,0	33,5	29,9	—
	Max. transv. diam., prox. end	26,0	26,3	23,1	22,4	20,4	—	25,7	—	—	—	—	—
Max. ant.-post. diam., dist. articulation	—	25,6	24,1	22,4	—	—	—	21,9	—	—	—	—	—
	—	28,1	26,0	c. 23,0	—	—	—	23,7	—	—	—	—	—
	Max. transv. diam., dist. articulation												

No complete innominate of *A. africanum* is known, the best specimen (L33341) comprising only the posterior part of the ilium and the acetabular region. The latter is similar to that of the *U. arctos* comparative specimen, and is distinguished only by its slightly larger size. There is, however, a greater dorsoventral constriction of the ilium anterior to the acetabulum, while the dorsoventral diameter of the posterior parts of the sacroiliac articulation is actually less than in the comparative specimen. *A. africanum* is more like *Ailuropoda* in this respect (see Davis 1964, fig. 59). The iliopectineal eminence is less prominent than in *U. arctos*, and in this respect it is also *Ailuropoda*-like. No other important features are observable in L33341, but the fact that it is more like *Ailuropoda* than *U. arctos* in at least two respects may be significant. The pelvis of the former is very different from those of other bears (Davis 1964: 113), and it is possible that that of *A. africanum* was equally distinctive.

The femur of *A. africanum* is represented by several fragmentary specimens, and a complete one (L40002) belonging to an aged and arthritic female (Fig. 20, Table 9). The latter specimen is considerably smaller and more slender than corresponding parts of male specimens, but is morphologically similar to them. It differs from the femur of the *U. arctos* comparative specimen in being slightly longer and relatively more slender.

The head of the femur is hemispherical, as in other ursids, while the neck is distinct and slightly longer than in *U. arctos*, but similar to that of Asian *Euarctos* and *Ailuropoda*. The greater trochanter is lower than the head and it is similar to the *U. arctos* femur in this respect. The gluteal tuberosity is very prominent in L40002 and terminates well below the level of the lesser trochanter, which is also prominent. The area of attachment of the quadratus femoris muscle between the lesser trochanter and gluteal tuberosity is well marked, as is the area of attachment of the adductor muscle, which extends about three-quarters the length of the very straight shaft. The distal end of the femur is essentially similar to that of *U. arctos*.

The femur of *A. africanum* is very different from that identified with *A. sivalense* by Lydekker (1884, pl. 29, fig. 1). This very curious specimen may be pathological.

The tibia of *A. africanum*, of which only one complete specimen (L45062) is known, is also very variable in size (Fig. 21, Table 9). As with the femur, L40002, the tibia is longer than that of the *U. arctos* comparative specimen, but in this instance it is also much stouter, evidently because L45062 belongs to a male. The proximal end of the tibia differs most markedly from those of ursines in having the tibial tuberosity and crest more prominent. This applies even in the case of specimens belonging to females (e.g. L50842). In addition, the proximal articular facets are relatively longer anteroposteriorly.

In *Ailuropoda* and ursines the lateral edge of the tibia shaft viewed anteriorly is bowed, with the tibial crest paralleling the proximal curvature. This, together with prominent lateral projections at the proximal and distal ends, 'increases the interosseous space between the tibia and fibula, and the total width across



Fig. 20. A-B. Anterior and posterior views of Langebaanweg *Agriotherium* femora. A. L40002. B. L40128. C. Medial view of L40002.



Fig. 21. Anterior and medial views of Langebaanweg *Agriotherium* tibia, L45062.

TABLE 9
Dimensions of Langebaanweg *Agriotherium* femora and tibiae.

	FEMORA				TIBIAE			
	L40043	L40128	L40002	L49889	L50841/ L50833	L45062	L40029	L40028
Overall length	—	—	425,0	—	—	378,0	—	—
Max. ant.-post. diam. of head	c. 57,5	54,1	48,4	—	—	—	—	—
Max. ant.-post. diam., proximal end	—	—	—	—	—	98,1	87,3	—
Max. transv. diam., proximal end	c. 128,0	111,5	98,0	—	108,5	100,1	c. 93,0	82,2
Max. ant.-post. diam., distal end	—	—	76,7	71,0	52,1	51,0	—	—
Max. transv. diam., distal end	—	—	c. 82,0	71,2	72,0	65,0	—	—

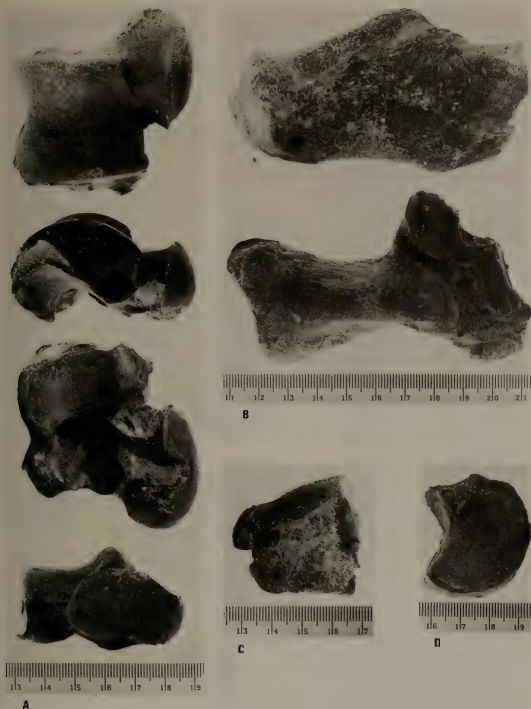


Fig. 22. Tarsal bones of Langebaanweg *Agriotherium*, L45062. A. Proximal, lateral, ventral and distal views of astragalus. B. Lateral and dorsal views of calcaneum. C. Dorsal view of cuboid. D. Proximal view of navicular.

the leg' (Davis 1964: 115). The tibia of *A. africanum* differs in having the proximal and distal lateral projections less prominent, and the shaft less bowed, which gives it a much straighter and more bilaterally symmetrical appearance in anterior view. The distal articular facet, like the proximal ones, has a relatively greater anteroposterior diameter than in ursines. The same applies to the proximal and distal fibula facets, while the fibula itself is much like those of ursines.

All the tarsal bones of *A. africanum*, except the mesocuneiform, ectocuneiform and tibial sesamoid, are known from at least one, and as many as eight specimens (Fig. 22, Table 10). The tibial sesamoid, like the radial sesamoid, was probably absent in this species. As with the carpals, the tarsals are essentially similar to their counterparts in Ursinae, and they, too, exhibit appreciable sexual dimorphism.

The astragalus is the best represented tarsal bone. It is distinguished from those of ursines principally by a longer neck. The available ursine astragali have a variably developed lip of bone projecting posteriorly from the base of the tibial facet, and which is most prominent medially. This lip of bone is absent in *A. africanum*, although in the specimens L45062 and L47533 there is a ventrally projecting lip of bone in this position. Since it effectively inhibits movement between astragalus and calcaneum, it is probably an abnormality caused by osteo-arthritis.

The calcaneum of *A. africanum* is also ursine-like, differing principally in having a relatively shorter and much stouter tuber calcis.

The remaining tarsal bones differ in only minor respects from their counterparts in *U. arctos*.

All the metatarsals of *A. africanum* are represented by at least one complete specimen (Fig. 23, Table 11). They are in general much stouter but only slightly longer than their counterparts in *U. arctos*. An exception is a small metatarsal I (L50771), evidently that of a female, which is of similar length and which is

TABLE 10
Dimensions of Langebaanweg *Agriotherium* tarsals.

	ASTRAGALI					
	L45062 (R)	L50765	L47533	L50766	L50770	L47910
Max. ant.-post. diam.	63,6	—	61,9	58,0	46,7	45,8
Max. transv. diam.	63,2	62,1	59,8	c. 56,5	51,2	43,7
Transv. diam. of tibial facet	44,9	c. 46,0	43,1	37,2	33,5	29,5
Transv. diam. of navicular facet	43,5	44,5	43,0	37,9	32,8	27,0
Max. dorsoventral diam.	40,4	—	37,2	35,3	28,8	27,5
	CALCANEUM		NAVICULARS		CUBOID	
	L45062		L50773	L45062	L45062	
Max. ant.-post. diam.	100,0		48,7	43,3	42,2	
Max. transv. diam.	64,5		38,7	38,2	34,9	
Max. dorsoventral diam.	56,4		20,5	17,6	35,9	
Max. transv. diam. of tuber calcis	45,7		—	—	—	

(R) = Right

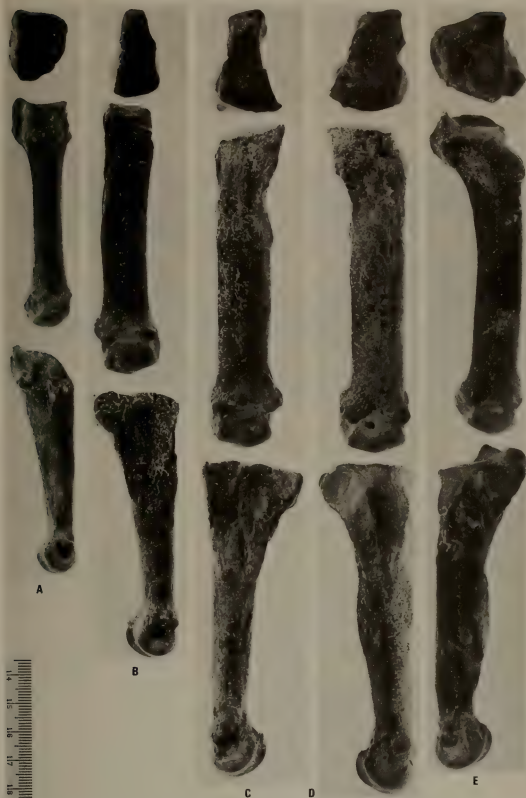


Fig. 23. Proximal, anterior and lateral or medial views of Langebaanweg *Agriotherium* metatarsals. A, I, L50787. B-E, II-V, L45062.

TABLE 11
Dimensions of Langebaanweg *Agriotherium* metatarsals.

	I			II			III	
	L50787	L47387	L50771	L48573	L45062	L40030	L45062	L30205
Overall length	81,5	—	70,1	103,1	94,4	92,0	110,6	107,9
Max. ant.-post. diam., proximal end	23,6	22,8	21,7	32,3	32,0	30,0	36,5	34,1
Max. transv. diam., proximal end	22,1	21,7	19,6	17,8	17,3	17,0	24,2	22,5
Max. ant.-post. diam., distal articulation	14,3	—	13,0	18,0	18,2	17,1	20,5	19,4
Max. transv. diam., distal articulation	17,5	—	14,4	20,7	21,2	19,6	22,2	21,1
	IV		L50812	V				
	L50824	L45062		L48572	L45062	L50829	L41108	
Overall length	—	116,4	—	119,5	115,5	—	—	
Max. ant.-post. diam., proximal end	39,2	35,4	32,1	31,1	30,8	29,6	27,3	
Max. transv. diam., proximal end	31,8	27,9	32,3	27,0	30,7	31,1	27,5	
Max. ant.-post. diam., distal articulation	—	20,6	—	19,7	21,0	—	—	
Max. transv. diam., distal articulation	—	23,7	—	c. 22,5	23,2	—	—	

more slender than that of the *U. arctos* comparative specimen. Morphologically there are no significant differences between the metatarsals of *A. africanum* and *U. arctos*.

The patella, sesamoids and phalanges of *A. africanum* are also *U. arctos*-like, although the 1st and 2nd phalanges of the former are relatively much shorter and stouter (Fig. 24).



Fig. 24. Dorsal and lateral or medial views of Langebaanweg *Agriotherium* phalanges, L45062, possibly of one digit.

DISCUSSION

The overall impression gained from the study of the skull and postcranial skeleton of *A. africanum* is of a large and heavily built animal which was unmistakably bear-like in its appearance (Fig. 25). It was undoubtedly plantigrade since its postcranial bones exhibit most of the characteristics found by Ginsburg (1961) to be indicative of this condition. The appreciable size variation observed is to be expected of a bear of such large proportions, since marked sexual dimorphism is characteristic of these animals (Kurtén 1955, 1966, 1967). Being typical of large ursids in this respect, it is of interest to compare *A. africanum* with better known species which belong in this category. They include *Ursus spelaeus*, *Tremarctos floridanus*, and *Arctodus simus*.

Of these species *A. africanum* probably resembled the North American late Pleistocene tremarctine, *Arctodus simus*, most closely. For example Kurtén (1967: 49, fig. 28) found that the skull of this short-faced bear 'shows a remarkable convergence with the great cats', which is also a feature of the skull of *A. africanum* (see p. 9 and Fig. 3). In overall size the male skull of the latter (L45062) is intermediate between those of female and male *A. simus* (see Table 1 herein and Kurtén 1967, table 5). In addition, the postcranial bones of *A. africanum* are similar in proportions to those of *A. simus*, although they differ in

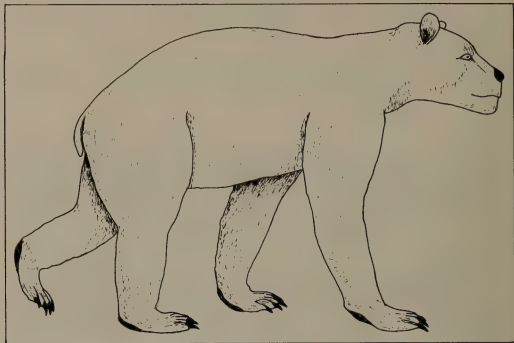


Fig. 25. Reconstruction of *Agriotherium*, adapted from one of North American *Arctodus simus* by J. Matternes (in Guthrie 1972).

some morphological details. In actual size the bones of *A. africanum* males compare closely with those of *A. simus* females (e.g. the Potter Creek Cave sample—see Tables 4–11 herein and Kurtén 1967, tables 10–25).

Unfortunately the skeleton of *A. africanum* is less well represented than that of *A. simus* and consequently cannot be analysed in as much detail. In view of the marked individual size variation in *A. africanum* it may be misleading to combine skeletal elements of different individuals in metric analyses. Nevertheless, this was done in several instances, one of which is presented here.

The isolated metatarsal I, L50787, which is evidently that of a male, was combined with the metatarsals II to V of L45062, also a male, in order to compare their relative lengths with the metatarsals of other ursids (Table 12). The similarity to the Potter Creek Cave *A. simus* sample is striking.

On the other hand, the calcaneum length expressed as a percentage of the longest metatarsal length of L45062 is 86.6, a figure which compares closely with the 86.5 of an *U. arctos* sample, and which is considerably lower than the figures for extinct tremarctines and *U. spelaeus*, which are over 100 (Kurtén 1966, table 36; 1967, table 27).

In spite of such deviations from the *Arctodus* pattern, *A. africanum* is like this genus and different from other later ursids in having relatively long legs. This characteristic, together with its specialized skull and dentition, is a highly significant departure from the typical ursid condition. Kurtén (1967: 50) interpreted *A. simus* as 'a predominantly carnivorous form', which may have

TABLE 12

Relative lengths of the metatarsals of some bears expressed as a percentage of the length of metatarsal V.

	I	II	III	IV	V
<i>Agriotherium africanum</i> . . . (L50787 + L45062)	71	82	96	101	100
<i>Arctodus simus</i> ¹ (Potter Creek Cave)	70	82	95	99	100
<i>Tremarctos floridanus</i> ¹ (males)	69	80	91	103	100
<i>Ursus spelaeus</i> ¹ (Salzofen)	63	78	88	98	100
<i>Ursus arctos</i> ¹ (Recent)	65	79	87	96	100

¹ Kurtén 1967, table 26.

'preyed on large contemporary herbivores', and although not 'truly cursorial it may have been capable of bursts of speed exceeding those of *U. arctos*'. These conclusions presumably apply equally well in the case of *A. africanum*.

The ecology and relationships of this species will be dealt with in more detail in following sections of this report.

PALAEOECOLOGY

The Langebaanweg *Agriotherium* assemblage is comprised of over 330 specimens, which represent a minimum of 14 individuals. Females are much less commonly represented than males, and no very young animals are known. Those postcranial bones belonging to immature individuals are probably all of young adults, while those of which teeth are known are all young or prime adults. Some specimens (e.g. L40002) show signs of osteo-arthritis, which suggests an advanced age for the individuals concerned. Bone pathology is otherwise rare, one notable exception being the metacarpal, L45448, which exhibits an osteitis of the proximal end, the cause of which is unknown.

All *A. africanum* specimens were found in, or closely associated with, river channel deposits. They occurred together with a wide variety of terrestrial, freshwater and marine vertebrates, which range in size from shrews to whales. Lists of most associated mammals have been given elsewhere (Hendey 1976, table 4; 1978, table 10). Associated birds will be listed by P.V. Rich (in preparation). Lists of lower vertebrates, which include cartilaginous and bony fish, amphibians and reptiles, have yet to be compiled. It is clear that *A. africanum* was an element of a rich and diverse fauna, with resemblances to both late Miocene (Turolian) faunas of Eurasia, and later African faunas. The Varswater Formation fauna includes descendants of taxa typical of the Eurasian late Miocene, with *A. africanum* included in this category, as well as ancestors of species which are now typically African.

A. africanum is one of the Varswater Formation taxa not recorded from the Quartzose Sand Member, the lowest of the three important fossil mammal-bearing units of the succession (Hendey 1976) (Table 13). The Quartzose Sand

TABLE 13

Depositional environments, characteristic sediments and fossil occurrences in the Varswater Formation, 'E' Quarry, Langebaanweg.

Dingle <i>et al.</i> 1979	Hendey 1976 and this report		DEPOSITIONAL ENVIRONMENTS	CHARACTERISTIC SEDIMENTS	FOSSIL OCCURRENCES
A-C D1	PPM, undifferentiated		marine littoral	phosphatic sand	some marine microfossils, vertebrates very rare
D3	I		river bank	clayey sand on phosphate rock	fossils abundant; seals and terrestrial vertebrates predominant
	II		river channel	quartz sand and fossil lag on, and in lee of phosphate rock	fossils abundant; seals and terrestrial vertebrates predominant
	III		intermediate between II and IV	quartz sand and fossil lag grading into carbonaceous sand and clay	fossils common; seals and terrestrial vertebrates predominant
D2	IV		marsh and pond	carbonaceous sand and clay, sometimes under quartz sand and clay horizons	fossils progressively less common south of III; only vertebrates recorded, but pollens probably present
D4	PPM, bed sub- 3aS		river channel and river bank	quartz sand and fossil lag grading upwards into phosphatic sand	fossils abundant, but becoming less common in phosphatic sand; terrestrial vertebrates predominant

E1	QUARTZOSE SAND MEMBER				QSM	I	floodplain, with associated microenvironments (e.g. pond, minor drainage channel)	quartz sand	fossils sometimes abundant; terrestrial vertebrates predominant
	E2	E3	E4	I(A)		possible variation of I, ? flood-plain closer to river channel	quartz sand	fossils sometimes common; terrestrial vertebrates predominant	
				II		marsh	carbonaceous sand and clay	fossils abundant; pollens pre-dominant, terrestrial vertebrates common	
				III		tidal flats	muddy silt	fossils abundant; marine, estu-arine and freshwater inverte-brates predominant	
E4	(IV)	? river channel (not exposed but probably exists south-east and south of quarry)	not known	not known					
	F	GM ₁ undifferentiated	rocky and sandy beach	phosphate rock gravel and quartz sand	fossils sometimes abundant; marine vertebrates and inverte-brates predominant				

Note. The subdivisions D2 and D3 and E1 to E4 (and their equivalents, PPM 3aN I to IV and QSM I to IV) are facies of sedimentary units (see Dingle *et al.* 1979, fig. 5).

Member deposits were laid down mostly on the floodplain of a river which then met the sea to the south or south-west of the existing 'E' Quarry. Many of the fossils from this unit are believed to represent the remains of animals which lived in the immediate vicinity (Hendey 1974: 349-353; 1976: 223-226). By contrast, most of the Pelletal Phosphorite Member fossils, including those of *A. africanum*, were washed into the area by the river, which was then following more northerly courses, first depositing bed 3aS and later bed 3aN (Hendey 1976: 226-230). Consequently, the *A. africanum* fossils are likely to be out of their natural environmental context, and there is no way of certainly establishing the nature of the preferred habitat of the species. Assuming that *A. africanum* was a terrestrial species, the number of possibilities is, however, limited, and there is some evidence which favours one of them.

The environment in the vicinity of Langebaanweg and in adjacent areas at the time of deposition of the Varswater Formation was clearly very different from that of the present (Hendey 1973). Long-necked giraffes (*Giraffa* sp.) were common, and, together with other large browsers such as a sivathere (*Sivatherium hendeyi*), a palaeotragine (*Palaeotragus* cf. *germaini*), and primitive proboscideans (*Anancus* sp., *Mammuthus subplanifrons*), indicate the presence of trees, probably in substantial numbers, and perhaps in the form of a riverine woodland. On the other hand, grazers such as alcelaphine antelopes (Gentry 1980 in press), an equid (*Hipparion* cf. *baardi*), and a rhinoceros (*Ceratotherium praecox*) indicate the presence of grasslands as well. Although there was evidently a variety of micro-environments in the area (Hendey 1976), it is only the major terrestrial habitats of woodlands and grasslands which need be considered in the case of *Agriotherium*.

Of the large herbivores, the one which occurs most commonly in the Quartzose Sand Member and bed 3aS of the Pelletal Phosphorite Member is *Ceratotherium praecox*, a grazer, while browsing giraffoids are very rare in the Quartzose Sand Member, and only slightly more common in bed 3aS. By contrast, *C. praecox* is either very rare, or absent, in bed 3aN, while giraffoids are astonishingly well represented. The implication is that either woodlands became a progressively more widespread habitat during deposition of the Varswater Formation, or that taphonomic factors were such that woodland species had their remains incorporated in the deposits with increasing frequency. Either way, the fact that *A. africanum* is not recorded from the Quartzose Sand Member, is rare in bed 3aS, and is relatively common in bed 3aN, suggests that it was a woodland species.

This conclusion has also been reached in respect of *Agriotherium* elsewhere. Kurtén (1968: 119) suggested that *Agriotherium* 'was probably a forest animal like most modern bears', while Wolff *et al.* (1973: 226) concluded that 'it does seem that specimens of *Indarctos* and *Agriotherium* are better represented at localities which have a greater representation of woodland forms'. The possible influence of habitat on the evolution of *Agriotherium* will be discussed later (see p. 70).

The habitat preference of *Agriotherium* may have been a factor which contributed to its comparatively poor fossil record, but this was almost certainly due largely to the habits of the animal. *Agriotherium* has long been recognized as an atypical ursid because it was apparently carnivorous rather than omnivorous. Carnivorous species of such gigantic proportions would of necessity have been rare animals, even under the most ideal conditions (Wolff *et al.* 1973). The same restriction would not apply in the case of more omnivorous bears, and for later species the 'fossil record is excellent; indeed, as regards the Pleistocene bears of Europe, almost incomparable' (Kurtén 1968: 119). An added factor in the case of the latter was that extreme climatic conditions during the Pleistocene led bears to use caves as retreats, with consequent concentration of their remains in caves. Such circumstances did not apply to *Agriotherium*, all remains of which are recorded from open sites dating from a climatically moderate period.

Although *A. africanum* has been said to be a well represented species, it is nevertheless one of the less common elements in the Langebaanweg assemblage, which is now comprised of the remains of many thousands of animals. Proportionately, *Agriotherium* may be no more common at Langebaanweg than it is at localities elsewhere.

Many of the Langebaanweg *Agriotherium* specimens were recovered in the course of mining operations, or by screening of bulk sediment samples mechanically removed from the mine. In these instances the original condition of specimens, associations of skeletal elements and body part representations cannot necessarily be determined. More significant from a taphonomic point of view is that material recovered from controlled excavations. Three such excavations yielded *Agriotherium* remains (Fig. 26, Table 14), and the relevant material is listed on pages 5-6.

The deposits in which this material occurred are noteworthy for the almost complete absence of a very coarse lithic fraction. Occasional pebbles of quartz, feldspar and the local phosphate rock do occur, but the sediments are generally made up of medium- to coarse-grade sands. Fine sands and clayey sands are also present. The larger elements of the lag gravels in bed 3aN are almost exclusively bones and teeth of vertebrates (Fig. 27). Consequently, those fossils transported by the river were not subjected to the destructive battering by, and against, cobbles and boulders, which is often a feature of this sedimentary environment. For about 30 km east of Langebaanweg there are few rock outcrops, the area being largely covered by the generally sandy deposits of the 'Sandveld' (see Talbot 1947; Visser & Schoch 1973). This means that in its lower reaches the river which was largely responsible for building up the Varswater Formation (Fig. 1) could have picked up little in the way of a coarse lithic fraction. In addition, its generally sandy bed would have provided a relatively smooth passage for organic materials in its load.

In fact the fossils of beds 3aS and 3aN show remarkably few signs of abrasion which could be ascribed to transport in sand-charged water over a



Fig. 26. Aerial view of past and present areas of exposure of bed 3aN in 'E' Quarry, Langebaanweg. 1-LBW-E 1975/1; 2-LBW-E 1976/1; 3-Dump 10; 4-LBW-E 1976/2; 5-Dump 9; 6-Dump 8; 7-Carbonaceous deposits; R-Phosphate rock outcrops; W-Wet season river channel; D-Dry season river channel.

sandy substratum. What abrasion there is may have developed after deposition rather than during transport (see below). This suggests that many of the fossils reached the vicinity of 'E' Quarry still protected by soft tissue, perhaps even as floating carcasses, and that disarticulation and dispersal of skeletal elements took place locally.

The bed 3aN *Agriotherium* specimens were recovered from deposits laid down in three distinct micro-environments. Those deposits exposed in the

TABLE 14

Controlled excavations in 'E' Quarry which yielded *Agriotherium* remains.

EXCAVATION NUMBER	SITE	DEPOSITIONAL ENVIRONMENT	STRATIGRAPHIC UNIT ¹
LBW-E 1975/1	TCWW Prom	river bank and river channel, with phosphate rock substratum	PPM 3aN I
LBW-E 1976/1	RP	river channel, with phosphate rock substratum	PPM 3aN II
LBW-E 1976/2	IWRP ²	river channel in lee of phosphate rock, with unconsolidated sand substratum	PPM 3aN II

¹ See Table 13.² Locality 5 of Dingle *et al.* 1979, fig. 2.

excavation LBW-E 1975/1 were laid down partly in the river channel and partly on the north bank of the channel. Channel deposits were sampled in both excavations LBW-E 1976/1 and 1976/2, the depositional environments differing only in that the former had a rock substratum and the latter a sandy one. In both the 1975/1 and 1976/1 areas the substratum was a phosphate rock horizon of up to 0,75 m thick. The third micro-environment was not sampled by controlled excavation, but was the source of a few *Agriotherium* specimens recovered in the course of mining operations. This was an extensive area of carbonaceous (peat-like) deposit over the southern (seaward) limit of the river channel. It was probably the area of accumulation of plant debris washed down by the river during flood times. During the dry season it formed the west bank of the river and was probably a marshy area with appropriate vegetation. The likely positions of the wet and dry season channels are indicated in Figure 26.

The bed 3aN deposits are overlain by the thick and extensive commercially exploited phosphatic sand, which was deposited in a marine littoral environment (Tankard 1975), and from which some fossil vertebrates, not including *Agriotherium*, are known (Hendey 1976: 230).

The fossils from LBW-E 1975/1, which were deposited close to or on the north bank of the river channel, were generally better preserved and less fragmented than those from the other two excavations. This applied particularly in the case of specimens not in direct contact with the phosphate rock substratum. In the area of LBW-E 1976/1 most of the deposit overlying the phosphate rock had been mined away, and the material recovered came from on, or close to the rock surface itself, particularly depressions therein. This material was for the most part very fragmented.

The greatest concentration of fossils in bed 3aN was in the area of LBW-E 1976/2. Here the deposits were laid down on an unconsolidated substratum (the Quartzose Sand Member) in the lee (west) of the phosphate rock exposed

in the other two excavations. Immediately adjacent to the phosphate rock a 60 cm thick horizon of fossils was accumulated (Fig. 27). This thinned out rapidly to as little as 10 cm westwards and southwards. Most of the fossils in this area were highly fragmented and in a poor state of preservation. This applies particularly in the case of the remains of larger species, of which giraffoids, especially *Sivatherium*, were by far the most commonly represented. By contrast the remains of aquatic vertebrates, with the seal, *Prionodelphis capensis*, being exceedingly common, tended to be in good condition, although their remains were often fragmented and skeletons disarticulated and dispersed.

As this fossil lag deposit thinned westwards and southwards, the clastic matrix became finer-grained, with an increasing clay component. Westwards the fossiliferous horizon terminated abruptly against another phosphate rock outcrop, but southwards it once again thickened and also spread out laterally in a south-westerly direction. There was also a rapid darkening in the colour of the clastic matrix, which coincided with a diminution in the occurrence of vertebrate fossils. These fossils occurred mostly as isolated, and often fragmented, teeth and bones, but associated parts of skeletons, including at least one of *Agriotherium*, are recorded. In the case of the latter, it is not known how complete they were, since all were chance discoveries made after disturbance of the deposit by mechanical excavators.

The darkening of the deposits southwards was caused by an increasing carbonaceous fraction, which was evidently derived from decomposed plant remains. This deposit was not a pure peat, the carbonaceous material having been mixed with a high proportion of sand and clay, but such peats might well have overlain the remaining carbonaceous deposit (see below).

The picture which emerges is that of a river which in times of flood carried in to the area remains of terrestrial vertebrates, sometimes as whole carcasses, depositing some along its banks and others in the channel itself. A major part of the load of vertebrate remains was deposited immediately after the channel passed over the western edge of a southward projecting tongue of phosphate rock. Another such outcrop about 30 m further west then deflected the channel southwards, where it spread out over a wide and flat area. Here it dropped the last of its organic load, this probably being comprised largely of easily transportable plant material. Some vertebrate remains also reached this area, but they are recorded only from the more northerly parts, that is, closest to the area where the main vertebrate load was dropped.

Although the vertebrate assemblage of bed 3aN is comprised largely of the remains of terrestrial species washed in by the river, marine vertebrates are also represented. In the case of the seal the number of individuals involved is substantial. The marine vertebrate remains are generally better preserved than those of terrestrial species, which suggests, not surprisingly, that they had suffered less transport. The seals, cetaceans, marine birds, bony fish, and sharks may all have been inhabitants of, or visitors to, the river estuary. This probably applied particularly during flood times when the influx of carcasses of terrestrial species



Fig. 27. LBW-E 1976/2 area of 'E' Quarry. Fossil lag deposit arrowed left, and phosphate rock outcrop sloping upwards in a north-easterly direction on the right. Scale in 5 cm divisions.

provided an abundant source of food for marine scavengers. Whether or not the seal was included in this category is not known. Seals may simply have been attracted by an increase in the numbers of scavengers such as fish and crustaceans, and would themselves have attracted predators such as sharks. Marine vertebrates were certainly in a position to have their remains caught up in, and dispersed by, the river's floodwaters.

During the dry season when the river was not in flood it is unlikely to have breached the phosphate rock outcrop which underlies the northerly and easterly parts of bed 3aN. Instead it would have been deflected southwards by this outcrop in the direction of bed 3aS, which was laid down during an earlier phase of the Varswater cyclothem. This would account for the fact that bed 3aS was abruptly truncated south of the phosphate rock outcrop. This truncation was not due solely to flood periods in bed 3aN times because bed 3aS terminated at least 25 m east of the first exposure of the carbonaceous deposit of bed 3aN, which is an indication of the width of the dry season channel. There may have been other distributaries of the river north of 'E' Quarry.

As indicated earlier, that area west of the dry season channel, where floodwaters had dropped their load of organic materials, probably took the form of a marsh.

Although the river probably still fed vertebrate remains into the area during the dry season, the number of specimens involved is likely to have been much lower. This raises a problem in connection with specimens collected between the principal exposures of bed 3aS and bed 3aN. There are relatively few such specimens, and their actual source is usually uncertain, since most were collected by mine workers in the course of their activities. This material has been recorded as being from bed 3aS, but it may actually belong with the bed 3aN complex of deposits. Those *Agriotherium* specimens with numbers between L40000 and L43000 fall into this category.

Fortunately there are no doubts about the source of *Agriotherium* specimens from the bed 3aN excavations, and those from the bed 3aN carbonaceous deposits, the latter being distinctive because of their dark colour. The only other fossils from 'E' Quarry in a similar state of preservation are those from the 'peat bed' of the Quartzose Sand Member (Hendey 1976: 218, table 2), and there was no possibility of material from these two deposits becoming mixed.

Although there can be little or no doubt as to how the bed 3aN *Agriotherium* remains reached the 'E' Quarry area, it is of interest to consider the nature of some of this material.

The partial skeleton, L45062, is interpreted as the remains of an animal which reached the point of its discovery as a complete, or nearly complete carcass. This carcass was deposited about 15 m west of the phosphate rock outcrop in the LBW-E 1976/2 area. It is virtually certain that at least some, and perhaps all, missing parts of L45062 were mined away, the parts recovered having come from an area of 2 to 3 m² immediately adjacent to a vertical face cut by a mechanical excavator. The remains were found in the lag deposit where

it was about 20 cm thick, and were centred on a depression on the unconsolidated substratum. The preservation of the remains was considerably better than that of the majority of surrounding fossils. Their good preservation, together with the unmistakable characteristics of *Agriotherium* bones and teeth, facilitated their recovery from a mass of thousands of fragmentary fossils.

It appears that after deposition of the carcass of L45062, flowing water scoured the depression beneath it. At the same time the carcass acted as an obstruction to coarse debris, causing it to settle in the immediate vicinity. Disarticulation and slight dispersal of skeletal elements followed decomposition of soft tissue. L45062 is unusual in being one of the few instances in the LBW-E 1976/2 area where parts of one individual were found in a good state of preservation, and with skeletal elements in close association. This was otherwise noticeable mainly amongst the seals, although in these instances the large number of individuals involved made it impossible to separate their skeletons.

The *Agriotherium* forelimb, L45063, was another instance where there was association of skeletal elements of one individual. This material was found in the same depression as L45062, but was readily distinguishable, having belonged to a smaller (female) individual. This forelimb must also have reached the area held together by soft tissue, perhaps with the scapula and most phalanges already detached. Although no two elements of this limb were found in articulation, the individual elements were less dispersed than those of L45062. The incomplete manus, L33160, from LBW-E 1975/1, was a similar occurrence to L45063.

Other *Agriotherium* specimens from the bed 3aN controlled excavations tended to be isolated occurrences of individual skeletal elements. Since they are generally well preserved and show few, if any, signs of abrasion, they, too, are likely to be from carcasses similar to that of L45062. However, in these instances there was greater dispersal of skeletal elements and associations were no longer obvious. The condition of isolated specimens was usually in keeping with the nature of the depositional environment. Long bones were invariably fragmented, but shorter and stouter bones, such as those of the manus and pes, were usually intact. The hemimandible, L45114, had lost the single-rooted teeth (incisors, P_3 and M_3), which are easily separated from the jaw, and the ascending ramus, which is more fragile than the mandibular corpus. The single-rooted canine was still in position, because the root of this tooth is large and slightly bulbous, and impossible to remove from the jaw without breaking the root or the bone enclosing it.

Also of interest from a taphonomic point of view is the post-mortem damage to specimens. This was clearly dependent on the micro-environment in which specimens were deposited.

The incomplete manus, L33160, was deposited close to, or on the north bank of the river in the LBW-E 1975/1 area. This specimen is remarkable because it provides evidence of the activities of hyaenas in this area. Like many of the fossils from 'E' Quarry, L33160 shows signs of having been chewed by



Fig. 28. Hyena-gnawed *Agriotherium* manus, L33160, from Langebaanweg. Arrows indicate areas of major damage.

a hyaena, and this was done while the bones were still articulated. The phalanges, metacarpal I and distal ends of the metacarpals II to V are lost, probably having been ingested by the hyaena concerned, and there are tooth-marks on some of the metacarpals adjacent to the missing parts. There is also damage on the scapholunar and unciform, but the magnum and trapezoid, which are largely enclosed by the other bones, are intact (Fig. 28).

The remains of at least six small hyaenas (*Ictitherium preforfex*) were recovered from LBW-E 1975/1. This species of hyaena, and perhaps others, probably scavenged the banks of the river for the remains of animals washed into the area. Hyaena-damaged bone was not uncommon in this area, another notable example being the skull of a seal with double punctate marks on the braincase. The lower canines of *Ictitherium preforfex* fit these punctate marks well.

Another specimen from LBW-E 1975/1, the metatarsal L30205, is remarkable in having on its shaft gnaw-marks apparently made by a small rodent (Fig. 29). This type of damage is rare amongst the fossils from 'E' Quarry.



Fig. 29. Rodent-gnawed *Agriotherium* metatarsal, L30205, from Langebaanweg. Arrow indicates area of damage.

Although rodent remains are generally common in the fossiliferous deposits of the Varswater Formation, this was not the case in the LBW-E 1975/1 area, where only bathyergids were represented in moderate numbers. Living bathyergids, which are fossorial, are known to gnaw at objects encountered in their tunnels, plastic water-pipes and telephone cables being items recently affected in this way in the south-western Cape Province. It is possible that a bathyergid tunnelling on the river bank was responsible for the damage to L30205.

Three distinct types of post-mortem damage are evident on the bones and teeth of the partial skeleton L45062. Most common is simple fracturing of bones, which is ascribed to movement after loss of soft tissue, and to subsequent compression by overlying deposit. Not surprisingly, it was the relatively delicate parts of the skull which were particularly affected by this fracturing. The second type of damage is abrasion, which was probably caused by sand-charged water

flowing over exposed parts of the partly buried skeleton. This type of damage is not uncommon on the fossils from 'E' Quarry, and a good example was mentioned elsewhere (Hendey 1970: 82, fig. 3).

The third type of damage was caused by fire, with affected bones and teeth being blackened, more badly fractured and less well preserved than unburnt bone (Fig. 30). This type of damage is also not uncommon on fossils from 'E' Quarry, and has been discussed elsewhere (Hendey 1974: 351; 1976: 224).



Fig. 30. Fire-damaged *Agriotherium* astragalus, L45062, from Langebaanweg.

It was previously assumed that fire-damage was caused by dry-season bush or grass fires. While this may sometimes have been the case, there are instances where the inferred depositional environment and nature of the damage is such that fires of another sort are likely to have been responsible. The fire-damage of L45062 is a case in point.

It is clear that this damage was done after the skeleton had been disarticulated, since severe fire-damage on one bone is not matched by damage to immediately adjacent parts of the skeleton. For example, the symphyseal region of the right hemimandible is fire-damaged and the incisors are lost, whereas the left hemimandible is intact in this region and the incisors are present. Similarly, the distal end and part of the shaft of the left ulna is damaged, but corresponding parts of the left radius are unaffected.

Assuming that the depositional environment of L45062 has been correctly interpreted, it is highly improbable, if not impossible that the random burning of parts of the skeleton could have been caused by a bush or grass fire. A more plausible explanation is that the fire-damage was caused by peat fires, a phenomenon which has been reported in a North American estuarine swamp by Staub & Cohen (1979). It was indicated earlier that the horizon in which L45062 occurred graded laterally into a peat-like deposit, and that pure peats may have overlain this horizon. Such peats, if they did exist, may have been prone to dry season fires like the American example cited above. Having burnt away they would have left no trace obvious to observers unfamiliar with such phenomena other than some underlying burnt bone.

Peat fires may also have led to the formation of hitherto unexplained deposits capping the peat-like sediments immediately south of the LBW-E 1976/2 area. Immediately overlying the 'peat' was a horizon of sand a few centimetres thick, which was recorded as being 'orange-brown' in colour and in this respect unlike any other sand body recorded before or since in 'E' Quarry. The 'orange-brown sand' was in turn overlain by a grey clay incorporating scattered sand grains. In the examples of peat fires recorded by Staub & Cohen (1979), and in other similar ones (e.g. Cypert 1961), ponds developed in depressions left in the peat after burning, and such ponds become a new and distinct depositional environment in the areas in question. If there was, indeed, a peat fire in the LBW-E 1976/2 area, the orange-brown sand and grey clay may represent sediment accumulated in a resultant pond, while the underlying carbonaceous deposit represents an unburnt residue of the original peat deposit. The carbonaceous deposit may have remained unburnt either because it was waterlogged or because its high non-carbonaceous content made it incombustible.

The grey clay is finely laminated, suggesting slow accumulation in still-water conditions, with individual sediment particles perhaps having been transported to the pond by wind. The origin of the orange-brown sand is not known. It was initially thought that it may represent the unburnt residue of the peat fire, but the occasional vertebrate fossils incorporated in the sand show no signs of having been burnt.

The existence and effects of peat fires at Langebaanweg are largely speculative, but they do provide a plausible explanation for hitherto unexplained, or unsatisfactorily explained, aspects of the fossils and the deposits.

The ecological role of *Agriotherium* is also relevant here. It was mentioned earlier that *Agriotherium* was a carnivorous animal and, judging from its dentition, it was better adapted to carnivory than almost all other later ursids. It is the nature of the posterior cheek teeth which are particularly significant in this respect, and since these teeth are better represented in *A. africanum* than in previously recorded *Agriotherium*, it is useful to examine them from a functional viewpoint.

The P⁴, M¹ and M² of *A. africanum*, and other *Agriotherium*, resemble one

another in having a series of prominent buccal cusps and less prominent lingual ones (Fig. 31). In all there are seven buccal cusps, three on P^4 and two on each of the molars, and they are in the form of a smooth curve, with the convexity directed buccally. In addition to being lower-crowned, the lingual cusps are less distinct and fewer in number, only five excluding the vestigial accessory cusps on the P^4 protocone lobe. These cusps are more or less in a straight line.

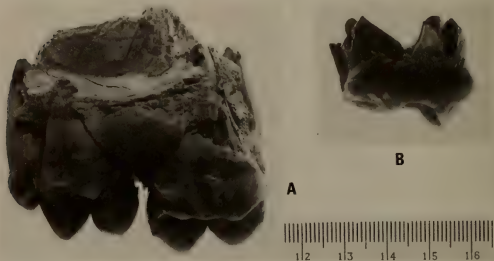


Fig. 31. Langebaanweg *Agriotherium* specimens showing prominence of buccal cusps. A. Lingual view of P^4 and M^1 . B. Anterior view of M^2 .

Judging from wear facets, the buccal cusps have a combined shearing and crushing function, with the former being predominant. The lingual cusps also have this double function, but in this instance the crushing function is predominant.

Much the same applies in the case of P_4 and the lower molars, in which the more prominent cusps are situated buccally. An exception is the large posterolingual cusp of the M_1 talonid. This cusp is, however, like the more buccal ones in developing an inclined shearing facet on its buccal side. The other lower teeth or cusps which develop inclined shearing facets buccally are the paraconid, protoconid and hypoconid of M_1 , the protoconid and hypoconid of M_2 , and the anterobuccal part of M_3 .

A most significant development relating to the emphasis of the buccal cusps in *A. africanum* is the reduction or loss of the anterolingual cusps of the M_2 's, L45114/L46563 and L50007. As far as is known this has not previously been observed in *Agriotherium*. It creates the impression that the M_2 of *A. africanum* was tending to become a second lower carnassial. Although smaller than the true carnassial, L45114/L46563 and L 50007 resemble this tooth in having the trigonid large and functioning essentially as a shearing element.

To have carried this evolutionary experiment to its logical conclusion

would have required continued suppression of the lingual cusps of P^4 , M^1 and M^2 , continued emphasis of the buccal cusps of these teeth, and a similar emphasis on the more buccal parts of the lower molars. This would have resulted in a sectorial dentition unique amongst Carnivora, but since no *Agriotherium* is known in which there was an advance on the *A. africanum* condition, it evidently served the needs of the genus adequately.

It is worth noting in this connection that a similar evolutionary path has been followed by the polar bear, *Thalarctos maritimus*. In this species the P^4 protocone is reduced or absent, the buccal cusps of M^1 and M^2 are relatively higher crowned than those of other ursines, while the lingual ones, including the M^2 talon, are correspondingly reduced. These dental characters reflect 'the carnivorous habits of the species and diverges from the omnivorous dentition of most other ursids' (Kurtén 1964: 4).

Whether *Agriotherium* was a predator or a scavenger is not known. Its large and cumbersome build suggests that the former alternative is less likely, although it may have been capable of hunting down at least some of the larger contemporary herbivores, such as the giraffids. The P^4 of *Agriotherium* has long been referred to as hyaenid-like (Falconer & Cautley 1836; Wagner 1837), and recently Wolff (1978: 4) has written that this tooth 'bears a striking resemblance in robustness to the teeth of the bonecrushing hyaenas'. This implies a belief that *Agriotherium* may have been a scavenger. However, in the hyaenas it is the more anterior cheek teeth which are enlarged to perform a bone-crushing function, and the enlarged cheek teeth of *Agriotherium* may have been too posteriorly situated to perform this function efficiently.

Irrespective of how its food was acquired, there can be no doubt that an abundance must have been available in the Langebaanweg area when it was inhabited by *Agriotherium*. There is evidence, however, which suggests that the Varswater Formation fauna dates from the latter part of the period which Kurtén (1971: 152) termed the 'climax of the Age of Mammals', and that even in its heyday it was becoming an anachronism. In fact, it is possible that the circumstances which led to the evolution of *Agriotherium* ultimately also caused its extinction.

The late Tertiary was a period of world-wide environmental change, with a general lowering of mean annual temperatures (Butzer 1971, fig. 2), which heralded the glacial-interglacial oscillations of the Pleistocene. Over wide areas of the Old World and the Americas, forests and woodlands were giving way to savannas and grasslands, and these changes had a profound effect on the character and composition of terrestrial vertebrate faunas (Webb 1977).

The Varswater Formation fauna provides evidence of these changes. For example, it includes two of the earliest alcelaphine antelopes yet recorded (Gentry 1980), and it is these bovids with their high-crowned teeth which are characteristic of the African savannas today. Similarly, an early ancestor of Africa's grazing rhinoceros (*Ceratotherium simum*) is recorded from Langebaanweg (Hooijer 1972). Palynological evidence from Langebaanweg, and elsewhere

in the south-western Cape Province, indicates that the modern Cape macchia (fynbos) vegetation was becoming established at this time, and that the climate was changing from 'Cool Wet' to 'Colder Drier' (Coetzee 1978: 121, fig. 2). There is even some as yet unpublished evidence to suggest that there was a marked fall in local sea temperatures during deposition of the Varswater Formation.

The immediate cause of the climatic and environmental deterioration in the Langebaanweg area and adjacent regions was the development of the Benguela Current System off the west coast of southern Africa and the consequent aridification of the adjacent land mass (Siesser 1978; Tankard & Rogers 1978). The development of the Benguela Current was in turn the result of major glaciation in Antarctica later in the Miocene (Kennett *et al.* 1975).

This period of climatic and environmental change must have influenced the Ursidae as much as any other mammalian group. During the Vallesian the ursids which inhabited Europe were generally relatively small omnivorous animals inhabiting forests and woodlands. That lineage which was to give rise to the Ursinae, and probably also the Tremarctinae, continued to be represented by small species during the Turolian. However, in the *Indarctos* lineage there was a marked increase in the size of the species during this period. In the following section of this report, evidence will be presented which indicates that *Indarctos* was the ancestor of *Agriotherium*, and consequently it is the *Indarctos* lineage, and the changes it underwent, which are relevant here.

By the Turolian (and its equivalents) the environment in mid-latitudes was in the process of change, with woodlands giving way to more open country (Kurtén 1971). Consequently, woodland plant foods such as fruits, nuts and berries, favoured by omnivorous ursids, were probably becoming less readily available. It is the larger species which would have been most adversely affected by this development, and thus Turolian *Indarctos*, and its counterparts elsewhere, may increasingly have been forced to adapt their diets to more abundant food sources. In this instance, the response was evidently in the direction of increased carnivory, with adaptations culminating in the evolution of *Agriotherium*.

During the Pleistocene a similar situation arose in respect of *Thalarchos*. At the onset of one of the glaciations, populations of *Ursus arctos* did not retreat southwards in advance of the ice, but instead adapted to the new conditions. Amongst other things, this involved a growing reliance on carnivory to replace the plant foods which had previously been part of its diet (Kurtén 1964; Hendey 1972).

The early ancestors of the giant panda, *Ailuropoda*, evidently responded to late Tertiary environmental change in a different way. They adapted their diet to include more readily available plant foods which had not necessarily figured in their diets previously. Thus arose the most herbivorous of all living ursids, whose main diet of bamboo shoots is varied by other plant foods when this is possible (Ewer 1973).



Fig. 32. The Chemfos Ltd mine property, Langebaanweg, Spring 1970.

By becoming a highly specialized herbivore, *Ailuropoda* ensured its survival, although latterly in diminishing numbers and in increasingly remote areas. On the other hand, by adopting carnivory, *Agriotherium* placed itself in direct competition with smaller and better adapted predators and scavengers for a declining food source (i.e. large woodland browsers), or one which was increasingly difficult for a large ambulatory carnivore to acquire (i.e. cursorial grazers of the savannas and grasslands). According to this hypothesis, the fate of *Agriotherium* was sealed by the factors which led to its origins.

The picture of the Langebaanweg *Agriotherium* which emerges is of a gigantic carnivore living at a time when vertebrate life flourished in the south-western Cape Province, and when the Langebaanweg area was well-watered and richly vegetated. The semi-arid environment of Langebaanweg today, devoid of indigenous trees and scarred by man's activities, is a poor reflection of the past (Fig. 32). Only some of the smallest of the carnivorous cousins of *Agriotherium*, namely foxes, polecats, mongooses and wildcats, still occupy the area and the prospects for their survival are limited.

RELATIONSHIPS OF *AGRIOTHERIUM*

The first *Agriotherium* specimens to be collected and recorded were several isolated teeth of an aged individual found at Montpellier in France early in the nineteenth century. These specimens, which are preserved in the Museum d'Histoire Naturelle, Geneva, were described by Cuvier (1822) under the name of '*Lophiodon* de Montpellier'. Stehlin (1907) gave an account of this historic material, whose true identity remained a mystery for many decades, and provided an indication of the difficulties originally encountered in correctly identifying and classifying specimens belonging to *Agriotherium*.

Although its ursid affinities were recognized by Falconer & Cautley (1836) on the basis of material from the Siwalik Hills of India, *Agriotherium* is in many respects an atypical member of the family. Of all the genera of Ursidae, it is *Agriotherium* and its herbivorous counterpart, *Ailuropoda*, whose relationships have been most controversial. The fact that *Agriotherium* has a poor fossil record, while that of its nearest relatives is not necessarily any better, has aggravated the problem. In addition, there has been a tendency to compare it with the ursine bears, which have long been well known, and this has further obscured matters, since the ursines and *Agriotherium* are only distantly related. Much the same applies in the case of *Ailuropoda*.

Hyaenarctos Owen, 1845, a junior synonym of *Agriotherium* Wagner, 1837, was the generic name in common use during the last century and the earlier part of the present one. Prior to the identification of *Indarctos* by Pilgrim (1913), '*Hyaenarctos*' was the name applied to species now referred to both *Agriotherium* and *Indarctos*. This is an indication that these two genera have many characters in common, a point made obvious by studies such as those of Frick (1926) and Matthew (1929). Pilgrim (1931, 1932) did much to clarify the situa-

tion, and thereafter, apart from occasional lapses (e.g. Viret 1939), the name '*Hyaenarctos*' fell into disuse, and Pilgrim's interpretation of the genera *Agriotherium* and *Indarctos* was generally accepted.

Pilgrim (1932: 42, 43) listed half a dozen characters which he believed distinguished these genera and concluded that '*Indarctos* appears to represent a distinct line of development from *Agriotherium*, in some ways more and in others less advanced than the latter', while '*I. punjabiensis* seems to some extent to bridge over the gulf between [them]'. In spite of the attention given by Pilgrim to the problem of distinguishing *Agriotherium* from *Indarctos*, and in determining their relationships to one another, and to other ursids, uncertainties have remained. Nevertheless, it has become common practice to include these genera in the subfamily Agriotheriinae, together with 'the basal genus of the family, *Ursavus*' (Kurtén 1966: 7).

Since *Agriotherium* and *Indarctos* fossils are not common, they, and the question of their relationships, have received only infrequent attention since Pilgrim's (1932) review. Such attention has been prompted on the one hand by descriptions of new material (e.g. Viret 1939; Kretzoi 1942; Tobien 1955; Thenius 1959; Hendey 1972; Crusafont & Kurtén 1976; Wolff 1978), and on the other by reviews of ursid inter-relationships and phylogeny (e.g. Erdbrink 1953; Thenius & Hofer 1960). On those rare occasions when the relationship between *Agriotherium* and *Indarctos* has been discussed, Pilgrim's (1932) opinion has been favoured. For example, both Erdbrink (1953, fig. 61) and Thenius & Hofer (1960, figs. 34-35) place these genera on separate lineages, and indicate derivation from an unknown common ancestor in the *Ursavus* group.

This theory is based on the belief that *Agriotherium* is the more 'primitive' (i.e. canid-like) of the two genera, which, since it survived later than *Indarctos*, must represent a distinct lineage. However, there is an alternative hypothesis. In previous studies on the Langebaanweg *Agriotherium* it was suggested that this genus was directly descended from *Indarctos* (Hendey 1972, 1977), an idea which was apparently first conceived by Schlosser (1899). Before examining this alternative in more detail it is worth noting what is known of the temporal ranges of the two genera.

In Europe *Agriotherium* is first recorded from the Ruscinian, while *Indarctos* is known only from the Vallesian and Turolian (Table 15). In North America *Agriotherium* is restricted to the late Hemphillian (i.e. 4.5-6.0 Ma) and *Indarctos* is recorded only from the latter part of the early Hemphillian (i.e. 6-7 Ma) (R. H. Tedford 1979, pers. comm.). In Africa the Langebaanweg *Agriotherium* is from a Ruscinian-equivalent fauna whereas the cf. *Agriotherium* from Sahabi (Boaz *et al.* 1979) is probably an advanced *Indarctos* in terms of current definitions, and is almost certainly a little older than the Langebaanweg species. The situation in Asia is still obscure, although it is now known that the Dhok Pathan of the Siwaliks, from which important *Indarctos* and *Agriotherium* specimens are recorded, spans an appreciable period during the late Miocene

TABLE 15

The occurrence of *Indarctos* and *Agriotherium* in Europe and the Middle East.

TAXON	LOCALITY	MAMMAL AGE ¹	MEIN ZONE ²	APPROX. AGE IN m.y. ¹
<i>Agriotherium insigne</i>	Montpellier	Ruscinian	14	5
<i>Indarctos atticus</i>	Concud	Turolian	—	9
	Samos		12/13	7-9
	Pikermi		12	9
	Maragha		—	7-8
<i>Indarctos arctoides</i>	Montredon	Late	10	10-11
	Orignac	Vallesian	—	—
	Pfaffstetten		—	—
	Westhofen		—	—
<i>Indarctos vireti</i>	Can Llobateres	Early	9	12
	Can Purull	Vallesian	—	—

¹ Berggren & Van Couvering 1974; ² Mein 1975.

and Pliocene (Pilbeam *et al.* 1977). Consequently, the Dhok Pathan representatives of these genera, whose taxonomy is controversial (see below), were not necessarily contemporaneous with one another. A similar situation may well exist in the case of *Indarctos* and *Agriotherium* from Chinese late Tertiary localities, with the former known from Localities 30, 31, 43 and 52, while *Agriotherium* is tentatively identified from Locality 13 (Kurtén 1952).

Indications are, therefore, that *Agriotherium* and *Indarctos* were not contemporaries, and when their age is known the former appears later in the fossil record. Consequently, their known temporal ranges are in accord with the theory that *Agriotherium* was descended from *Indarctos*.

While its relationships to *Agriotherium* may be controversial, the history of *Indarctos* itself is now reasonably well documented. It apparently had its origins in Europe during the Vallesian, having stemmed from an *Ursavus*, and subsequently spread through Asia and into North America (Thenius & Hofer 1960), as well as to Africa (see above). Differing interpretations of inter-generic relationships are possible. For example, Crusafont & Kurtén (1976) suggested that *I. vireti* was ancestral to both *I. arctoides* and *I. atticus*, whereas *I. arctoides* is here regarded as an intermediate between the other two species. Crusafont & Kurtén (1976: 15) further suggested that *I. anthracitis* 'may be a precociously specialized form'. This species is, indeed, unusual, perhaps because it evolved in isolation on a Tethyan island, but it is largely irrelevant to present considerations. Recorded Asiatic *Indarctos* are either close to *I. atticus* or more advanced, while North American *Indarctos* is more advanced than *I. atticus*.

Irrespective of the actual inter-relationships of *Indarctos* species, there is no doubt that *I. vireti* is a generalized and early form, whereas *I. atticus*, and Asian and North American *Indarctos* are more specialized and younger in age. For example, Crusafont & Kurtén (1976: 15) noted that *I. atticus* is 'more advanced [than other European *Indarctos*] with larger cheek teeth, more reduced premolars, heavy and powerful jaws, and ursine limb proportions'.

It follows that if *Agriotherium* were descended from *Indarctos*, then the evolutionary trends evident in the *I. vireti*-*I. atticus* lineage are likely to have been continued in the hypothetical *Indarctos*-*Agriotherium* lineage. This is, indeed, the case, and Crusafont & Kurtén's comments quoted above apply equally well to *Agriotherium* relative to *I. atticus*. Such general trends do not necessarily constitute proof of a direct phylogenetic relationship between the two taxa.

Much more convincing evidence comes from an examination of certain tooth and skull characters in advanced *Indarctos* (i.e. those between 6 and 9 m.y. old), and early *Agriotherium* (i.e. those that are, or probably are, about 5 m.y. old). Examples of the latter are *A. africanum* from Langebaanweg, *A. insigne* from Europe (Montpellier), and *A. palaeindicum* from the Siwaliks. Advanced *Indarctos* includes *I. atticus* from Europe (Samos) and Iran (Maragha), *I. punjabiensis* from the Siwaliks, and North American *Indarctos*. All recorded specimens of the latter are here referred to the species *I. oregonensis* (see p. 101).

The classification of material referred to some of the above species has long been complicated by specimens which exhibit a combination of characters 'typical' of both genera. Pilgrim (1932: 44-46) discussed such a problem involving three incomplete mandibles from the Dhok Pathan of the Siwaliks (GSI-D8, D9, D10), and although he found it 'difficult to give a definite answer', he decided to reverse the identifications suggested by Lydekker (1884). Pilgrim's identifications are accepted here, with D8 assigned to *Agriotherium palaeindicum*, while D9 and D10 are assigned to *Indarctos punjabiensis*. The latter has since been recognized as one of the more advanced representatives of *Indarctos* (Thenius 1959), while *A. palaeindicum* is one of the more primitive representatives of *Agriotherium* (Hendey 1977).

It is highly likely that more will yet be written on the identity of the Siwaliks' *Indarctos* and *Agriotherium*. Both Pilgrim and Lydekker may have been incorrect in their interpretation of GSI-D8, D9 and D10 (and other specimens) since they could represent a single species which was no more variable than the Langebaanweg *Agriotherium*. The anomalous situation in respect of *I. punjabiensis* and *A. palaeindicum* will be repeatedly evident in the discussions which follow. The study of new and well provenanced material from the Siwaliks may resolve a situation which is beyond satisfactory resolution on the basis of available evidence.

Whatever the final outcome of this controversy, the fact that specimens can with some justification be identified with either *Indarctos* or *Agriotherium* is here regarded as highly significant, with specimens such as GSI-D8, D9 and D10 being interpreted as 'intermediates' between 'typical' *Indarctos* and 'typical' *Agriotherium*. The present study has shown that such 'intermediates' are more common than has hitherto been supposed. The characters which the two genera have in common, coupled with apparent evolutionary trends linking them, provide surprisingly good evidence for the transition of *Indarctos* to *Agriotherium* considering the relatively poor fossil record of the taxa concerned.

Indarctos-Agriotherium 'intermediates' are included in the *A. africanum* assemblage, while an undescribed *A. insigne* specimen from Montpellier (NMB-MP549) and the recently described *Indarctos* skull from Florida (Wolff 1978) are also in this category. The Florida skull is perhaps the best single recorded specimen which is 'intermediate' between 'typical' *Indarctos* and 'typical' *Agriotherium*. The age of this specimen is 'late Hemphillian' (Wolff 1978: 1), and it probably dates back about 6 m.y. It is certainly younger than the Samos *I. atticus* skulls described by Helbing (1932) and Thenius (1949, 1959), and it is much younger than the skull of *I. vireti* from Spain (Crusafont & Kurtén 1976). On the other hand, it is probably a little older than the skull of the Langebaanweg *A. africanum*.

Judging from the few measurements given by Wolff (1978), and from illustrations, the Florida skull is appreciably larger than that of *I. atticus*, which in turn is larger than that of *I. vireti* (Crusafont & Kurtén 1976). The trend of increasing size with time in the *Indarctos* lineage is clearly illustrated by these specimens. This trend was continued with the evolution of *Agriotherium*, since the skull of *A. africanum* is, in some respects at least, still larger than that of the Florida *Indarctos*. In respect of size the Florida skull is probably closer to that of *A. africanum* (and *A. sivalense*) than the three described skulls of European *Indarctos*.

The general similarity between the skulls of the Florida *Indarctos* and *A. africanum* was discussed earlier (see pp. 9-16), while the differences between them can all be ascribed to the more advanced condition of the latter. The advances are probably all related to the larger size of the *A. africanum* skull, and to modifications of its masticatory apparatus.

Judging from the Florida *Indarctos* and *A. africanum* skulls, the following are the most significant cranial characters shared by advanced *Indarctos* and *Agriotherium*:

1. Snouts relatively short and broad.
2. Zygomatic arches very stout and of similar shape.
3. Sagittal crest very high.
4. Overall similarity of the basicranial regions, particularly the absence of the alisphenoid canal, and the positions of the oval, postglenoid and other foramina.

In respect of the development of the snout, zygomatic arches and sagittal crests, the Florida *Indarctos* is intermediate between *I. atticus* and *A. africanum*. The basicranial region of *I. atticus* is similar to those of the other two skulls, and, according to Crusafont & Kurtén (1976), the basicranial region of *I. vireti* is similar to that of *I. atticus*. *I. vireti* is more primitive, however, in having the 'facial part of the skull . . . relatively much longer than in *I. atticus*' (Crusafont & Kurtén 1976: 10).

The relatively short snout of *Agriotherium* goes together with a relatively short palate, which is of interest because Kurtén (1964: 22) found that the

palate of the polar bear, *Thalarctos*, is slightly shorter than that of the brown bear, *U. arctos*, a pattern which he was not 'able to match . . . in any other bear population'. Evidently the *Indarctos*-*Agriotherium* example was not taken into account, but it is a parallel to *U. arctos*-*Thalarctos* in this respect. Kurtén (1967) subsequently noted that, like *Thalarctos*, a short and broad snout characterizes *Arctodus*, another ursid which is convergent with *Agriotherium* (see p. 51).

Another apparent similarity between the skulls of *Agriotherium* and *Thalarctos* is that in lateral view they have a relatively straight profile, with the sagittal crest prominent (Erdbrink 1953). It was on this basis that Wagner (1837) proposed the name *Agriotherium* for the *Ursus sivalensis* of Falconer & Cautley (1836) (see Erdbrink 1953: 557). *Thalarctos* is like *Agriotherium* and *Arctodus* in being a carnivorous animal descended from an omnivorous ancestor, and other parallels between them will be mentioned below.

The presence of a premaseteric fossa in the mandible of *Agriotherium*, and its absence in *Indarctos*, is an important distinguishing characteristic, the significance of which has prompted much published and unpublished comment. In one recent account it was erroneously stated that the premaseteric fossa is also characteristic of *Ursavus* (Hendey 1977), an error stemming from Frick (1926: 99), citing Wegner (1913). In fact, *Ursavus*, like *Indarctos*, lacks this fossa, and it is thus peculiar to *Agriotherium* in the hypothetical *Ursavus*-*Indarctos*-*Agriotherium* lineage.

The premaseteric fossa is important from a phylogenetic point of view, since it, like other 'characteristics', may not be an invariably diagnostic feature of *Agriotherium*. For example, it is absent from at least one mandible which has been assigned to *Agriotherium*, namely, the *A. palaeindicum* specimen GSI-D8. On the other hand, in the Samos *I. atticus* specimen described by Thenius (1959) (NMW-Samos 1912, 29), there is a slight depression in the premaseteric region which could be an incipient fossa. No such fossa, however, has been reported in more advanced *Indarctos*, such as that from North America.

Thenius (1959) pointed out that most of the *Indarctos* mandibles then known were either incomplete or belonged to immature individuals, and that the premaseteric fossa was either not observable or absent. This fossa clearly is an ontogenetic character, since in the Langebaanweg assemblage it is well developed only in older individuals (e.g. L45062), and is shallow in the mandible of a young adult (L45114) (Fig. 33).

A premaseteric fossa is otherwise known amongst ursids in Hemicyoninae and Tremarctinae. Although the early history of tremarctines is not well known (Thenius 1976), there is nothing to indicate that they and the hemicyonines are closely related. Consequently, it is certain that the premaseteric fossa in these two groups was evolved independently. There is thus no reason to suppose that its presence in *Agriotherium* is indicative of a close relationship with either the Hemicyoninae or the Tremarctinae. Since the significance of the premaseteric fossa in ursids is not known (Davis 1955), there is no way of knowing why it should develop in some lineages and not in others.

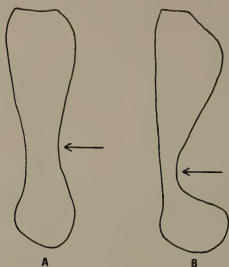


Fig. 33. Dorsoventral cross-sections of Langebaanweg *Agriotherium* hemimandibles with arrows indicating premaseteric fossae. A. L45114. B. L45062.

The teeth of *Indarctos* and *Agriotherium* provide much evidence in support of the theory that they are directly related.

As is often the case with carnivore incisors and canines, little of significance emerged from a study of these teeth in *Indarctos* and *Agriotherium*, except that they are essentially similar morphologically. The I^1 and I^2 are perhaps the most distinctive of the anterior teeth in *A. africanum*, and they are closely matched by those of the *I. atticus* specimen from Samos described by Helbing (1932, fig. 2) (NMB-Sam31). The anterior teeth of *Agriotherium* are distinguished from those of *Indarctos* principally by their larger size, this being a reflection of the overall size differences between the two genera.

It is worth noting in this connection that since the Agriotheriinae, like other ursids, exhibit appreciable sexual dimorphism, it is possible that large males of advanced *Indarctos* were of similar size to, and perhaps even slightly larger than, small *Agriotherium* females. For example, in terms of overall size the maxillary fragment of a small *A. insigne* specimen from Montpellier (NMB-MP549) is virtually identical in size to corresponding parts of the Vienna *I. atticus* specimen (NMW-Samos 1912, 29) (Fig. 34). Similarly, the Florida *Indarctos* skull is in some respects as large as that of the Langebaanweg *Agriotherium*, which belongs to a male, and would therefore have been larger than those of *A. africanum* females. Thus size alone may not necessarily be a reliable criterion for distinguishing the two genera.

One of the general trends in ursid evolution has been the emphasis on the development of the posterior cheek teeth, and the reduction in size or even loss of the anterior premolars (P_1 - P_3). More reduced premolars is one of the charac-



Fig. 34. Upper cheek tooth rows of *Indarctos atticus*, NMW-Sam1912/29 (left) and *Agriotherium insigne*, NMB-MP549 (right). Drawn from casts.

ters which distinguishes *I. atticus* from the earlier *I. vireti* (Crusafont & Kurtén 1976). In *I. atticus* P_1^1 and P_2^2 are apparently always single-rooted, while P_3^3 usually have two roots, although P_3 may sometimes have only one root (Thenius 1959). In the Florida *Indarctos* P_1 and P_2 are single-rooted, and P_3 is double-rooted (Wolff 1978).

Judged on the basis of the Langebaanweg sample, the anterior premolars of *Agriotherium* had undergone even further reduction, since in this instance all are invariably single-rooted and as many as two of a series may be lost (Table 16). This sample does not, however, exhibit one of the extremes in anterior premolar development encountered in *Agriotherium*. The Montpellier *A. insigne* specimen, NMB-MP549, is like advanced *Indarctos* in having a

TABLE 16
Anterior premolars in *Agriotherium* from Langebaanweg.

		P ¹	P ²	P ³	P ₁	P ₂	P ₃
L41404	. .	p	p	p	—	—	—
L50003	. .	—	—	—	p	p	p
L50445	. .	—	—	—	p	p	p
L40044	. .	—	—	—	p	a	p
L50004	. .	—	—	—	p	a	p
L50903	. .	—	—	—	p	a	p
L45062	left	p	a	p	p	a	p
	right	p	a	p	p	a	a
L45114	. .	—	—	—	a	a	p

p = present; a = absent.

double-rooted P³ set transversely in the jaw. It is especially reminiscent of the Vienna *I. atticus* specimen in this respect (Fig. 34), the only difference being that the principal cusp in the latter is slightly more distinct. The P³ of NMB-MP549 is unlike that of any other recorded *Agriotherium*.

By contrast, the Vienna *I. atticus* specimen is *Agriotherium*-like in having the P₁ to P₃ reduced to single-rooted teeth.

Thus, in respect of anterior premolar development conditions typical of advanced *Indarctos* may occasionally be found in *Agriotherium*, and vice versa. In addition, the anterior premolars of *Agriotherium* are morphologically similar to those of advanced *Indarctos*, except for the slightly more distinct principal cusps in the latter. This is a primitive characteristic since the principal cusps of the anterior premolars of *I. atticus* are in turn less well developed than those of *I. vireti*.

The P₄'s of advanced *Indarctos* and *Agriotherium* are also almost indistinguishable in terms of their basic morphology. Differences in detail are probably no greater than those in the Langebaanweg *Agriotherium* sample, which includes one specimen (L50445) with the principal cusp configuration resembling that in the *I. atticus* specimen, NMB-Sam31 (Fig. 35). Of particular significance is the tendency in *Indarctos* for the development of a postero-internal bulge in the cingular region. This feature is well developed in the Maragha *I. atticus* specimen (De Mecquenem 1925). In *Agriotherium* the postero-internal bulge on P₄ is comparably developed, whereas it is absent or much less pronounced in all other ursids.

The principal differences between the P₄'s of advanced *Indarctos* and *Agriotherium* are that the latter are higher crowned and tend to be larger in

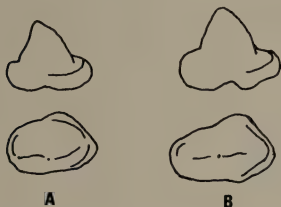


Fig. 35. Buccal and occlusal views of P_4 's.
A. *Indarctos atticus*, NMB-Sam31 (after Helbing 1932, fig. 3). B. Langebaanweg *Agriotherium*, L50445.

overall size. All the posterior cheek teeth of *Agriotherium* are higher crowned than their counterparts in *Indarctos*, although the Florida *Indarctos* specimen may be an exception in this respect. Apparently the crown height increase in the *Indarctos*-*Agriotherium* lineage was more or less in proportion to the overall increase in the size of the taxa concerned.

A likely parallel of this situation is that involving *Thalarcos*, which has relatively higher crowned posterior cheek teeth than *Ursus arctos* (Kurtén 1964).

In the case of the upper carnassial (P_4), it is the nature of the protocone lobe and the development of the parastyle which are of particular phylogenetic significance.

As a general rule the P_4 of *Agriotherium* is distinguished from that of *Indarctos* by the presence of a parastyle. However, some specimens of *Indarctos* do have a P_4 parastyle, although it is usually less prominent than that of *Agriotherium*. For example, this cusp is present in *I. atticus* from Conclud (Crusafont & Kurtén 1976) and Samos (Helbing 1932; Thenius 1959), *I. punjabiensis* from the Siwaliks (Lydekker 1884), and North American *Indarctos* (Merriam *et al.* 1925; Merriam & Stock 1925; Wolff 1978). The parastyle is particularly well developed in some North American specimens (e.g. the Florida skull), which are younger than European *I. atticus*. This cusp is absent in the still older and more primitive *I. arctoides* and *I. vireti*. There was thus a tendency for the development of a P_4 parastyle in the *Indarctos* lineage, and this was continued in the presumed descendant, *Agriotherium*, in which this cusp is always present and well developed.

As far as is known the only other ursids in which the P_4 parastyle is present are *Ursavus depereti* and its possible descendant, the giant panda, *Ailuropoda melanoleuca* (see p. 96).

The situation in respect of the P_4 protocone lobe is slightly different, although equally informative. According to the Crusafont & Kurtén (1976: 8)

there was a tendency for *I. vireti* to develop an antero-internal cusp on the P⁴, a situation which 'is not uncommon in *I. arctoides* and *I. atticus*'. This cusp is also present in the *I. punjabiensis* specimen, GSI-D6, although in this instance it is rather small (Lydekker 1884). In the younger and more advanced North American *Indarctos* this cusp is either reduced (Wolff 1978) or absent (Merriam & Stock 1925). This indicates that while a double-cusped protocone lobe is characteristic of most *Indarctos*, there was a tendency for the antero-internal cusp to be reduced or lost in advanced forms.

By contrast, an antero-internal cusp is found only in some of the earlier Old World representatives of *Agriotherium*, namely, *I. insigne* from Montpellier (NMB-MP549) and the Langebaanweg *A. africanum*. In the case of the latter, this cusp is best developed in the holotype, L2045, from bed 3aS, which predates those *A. africanum* P⁴'s from bed 3aN in which the antero-internal cusp is small or absent.

Indications are, therefore, that early forms of European and African *Agriotherium* still had an antero-internal cusp on P⁴, but this was soon reduced and lost. On the other hand, no Asian or North American *Agriotherium* is known to have had this cusp, which had already been reduced and lost in the advanced *Indarctos* of these continents. This suggests that the *Indarctos*-*Agriotherium* lineage may have had at least two geographically separated branches, one in Europe and Africa and the other in Asia and North America, which in respect of their P⁴ protocone lobes evolved at different rates. The implications of this possibility will be discussed later (see pp. 101-4).

Reduction of the P⁴ protocone is a characteristic of the *Ursus*-*Thalarchos* lineage (Kurtén 1964), and in South American *Arctodus* (Kurtén 1967). This is another example of a parallel development in *Agriotherium*, *Thalarchos* and *Arctodus*.

Once again a double-cusped protocone lobe is otherwise known only in *Ursavus depereti* and *Ailuropoda*, although in these taxa the morphology of the lobe is somewhat different (see p. 96).

As with the upper carnassial, the lower one (M₁) is an important tooth in indicating the origins of *Agriotherium*. There is, however, a complication with M₁, although in the final analysis its phylogenetic significance is not diminished. The complication concerns the identification of the posterolingual cusps of this tooth.

The cusp of the *Agriotherium* M₁ which has invariably been identified as the metaconid may in reality be the entoconid. If this is, indeed, the case, then the metaconid of the *Agriotherium* M₁ is either reduced or absent, usually the latter.

Both the metaconid and entoconid are present and well developed in *Ursavus* and *Indarctos*, although with time the metaconid becomes a progressively less prominent feature of M₁, since it is reduced in size relative to the entoconid and is increasingly overshadowed by the protoconid. In *U. primaevus* the metaconid is larger and more prominent than the entoconid, and is only

slightly less high-crowned than the protoconid (e.g. Crusafont & Kurtén 1976, fig. 13). Much the same applies in the case of *I. vireti* and *I. arctoides*, except that in these species the metaconid and entoconid are of comparable size (Crusafont & Kurtén 1976, fig. 2; Tobien 1955, fig. 3). In *I. atticus* the metaconid is much less prominent than the protoconid, but is still of similar size to the entoconid (Helbing 1932, fig. 3).

In the smallest of the *A. africanum* M₁'s (L50006) what is interpreted as a vestigial metaconid is still present. It is completely overshadowed by the protoconid, and, unlike its counterpart in *I. atticus*, is smaller than the entoconid. The metaconid is absent in all other M₁'s from Langebaanweg, and, apparently also from all other recorded *Agriotherium* M₁'s. The progressive reduction and eventual loss of the M₁ metaconid in the *Ursavus-Indarctos-Agriotherium* lineage is illustrated in Figure 36.

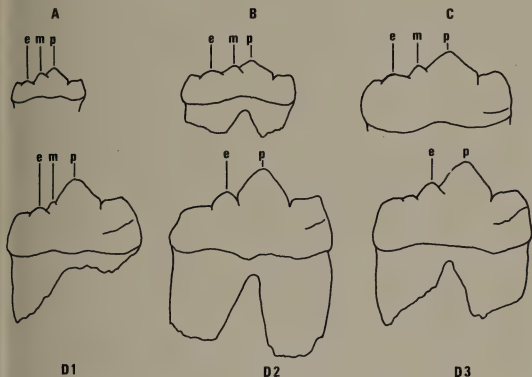


Fig. 36. M₁'s. A. *Ursavus primaevus* (after Crusafont & Kurtén 1976, fig. 14). B. *Indarctos arctoides* (after Tobien 1955, fig. 3). C. *Indarctos atticus* (after Helbing 1932, fig. 3). D. Langebaanweg *Agriotherium* (D1—L50006; D2—L50004; D3—L50446). All are lingual views except C, which is a buccal view with the buccal talonid cusps omitted. e—entoconid; m—metaconid; p—protoconid.

If the largest of the posterolingual M₁ cusps in *Agriotherium* is indeed the entoconid (i.e. a talonid cusp), rather than the metaconid (i.e. a trigonid cusp), this would account for Tobien's (1955: 14) observation that the 'Metaconid' of *Agriotherium* is 'niedriger und starker zurückgeschoben', while in *Indarctos* it is

'höher und näher an das Protoconid gestellt'. The cusp which Tobien believed to be the metaconid in *Agriotherium* may simply be a well-developed entoconid in more or less its usual position, while in *Indarctos* the metaconid was correctly identified as such, and it, too, is in its usual position.

The metaconid in *Indarctos* has a counterpart on the buccal side of the talonid, this being a small cusp situated between the protoconid and hypoconid. It is present in *I. vireti* (Crusafont & Kurtén 1976), *I. atticus* (Helbing 1932), *I. oregonensis* (Dalquest 1969), and other specimens, although traces of its presence may be obliterated by wear. A vestige of this cusp may be represented in the *A. palaeindicum* specimen, GSI-D8, by a slightly inclined ridge anterior to the hypoconid. A similar ridge is present in the M_1 of *A. africanum*, although in this species it takes the form of an undemarcated horizontal extension of the hypoconid. It meets with the posterobuccally directed keel of the protoconid. L50006 is also unusual in lacking this keel and in having the hypoconid ridge linked directly with the vestigial metaconid.

The reduction and loss of the M_1 metaconid in the *Indarctos*-*Agriotherium* lineage thus appears to have been accompanied by reduction and loss of its buccal counterpart. The impression gained is that these cusps were 'absorbed' by the protoconid, which is considerably enlarged in *Agriotherium*. This is a manifestation of the development of the shearing cusps (paraconid and protoconid) at the expense of the crushing cusps (talonid cusps) in the *Indarctos*-*Agriotherium* lineage.

It is possible, however, that the traditional interpretation of the large posterolingual M_1 cusp in *Agriotherium* as the metaconid is correct. Another of the Langebaanweg specimens, L50446, is unusual in having the largest of the posterolingual cusps flanked posteriorly by two smaller cusps, whereas in all other specimens there is only one such cusp. An almost exact match of L50446 is the M_1 of the *A. palaeindicum* specimen, GSI-D8 (Lydekker 1884). If the largest of the posterolingual cusps in these specimens are metaconids, then the smaller cusps immediately posteriorly would be the entoconids. It would, therefore, be the entoconid which is lost in other *Agriotherium* M_1 's, and this, rather than the loss of the metaconid, would have characterized the *Indarctos*-*Agriotherium* lineage. This hypothetical link would then be supported by the observation that the entoconid is as well developed in *Agriotherium* specimens such as L50446 and GSI-D8 as it is in some advanced *Indarctos* (e.g. *I. oregonensis*—Dalquest 1969, fig. 4).

In the case of the first alternative suggested above, the two smaller posterolingual cusps in L50446 and GSI-D8 would be interpreted as a duplication of the single cusp in this position in other *Agriotherium* M_1 's.

A first-hand examination of all relevant specimens may be necessary before deciding which of the above alternatives is likely to be correct. Irrespective of which applies, a transition from the typical *Indarctos* condition to that typical of *Agriotherium* is documented by specimens from the Siwaliks and Langebaanweg.

Another trend evident in the lower carnassials of *Indarctos* and *Agriotherium* is that of a reduction in their relative lengths with time (Table 17). Only the problematical Siwaliks' specimens GSI-D8 and D9 are anomalous in terms of their length: breadth ratios.

The arrangement and morphology of the M¹ cusps in advanced *Indarctos* and *Agriotherium* is virtually identical. The M¹ of *A. africanum* differs from that of *I. atticus* only in being relatively shorter and higher crowned, although it may be indistinguishable from more advanced *Indarctos* (e.g. the Florida specimen) in these respects.

In most, and perhaps all, *Indarctos* M¹'s the posterior keels of the metacone and hypocone are linked across the posterior end of the tooth by a low ridge of enamel. This feature is present but less obvious in *A. africanum*, and probably all other *Agriotherium*, and this region of the tooth also differs in being noticeably shorter than in the corresponding part of the *I. atticus* M¹. In other words, there is a very short 'talon' region in the latter, and it is reduction of this feature which contributes to the overall shortening of M¹ in *Agriotherium*.

TABLE 17

Length : breadth ratios of *Indarctos* and *Agriotherium* M₁'s.

TAXON	LOCALITY and/or NUMBER	LENGTH	BREADTH	L : B	MEANS
<i>Agriotherium africanum</i>	L45062	39,7	23,0	1,73 : 1	1,82 : 1
	L45062	39,7	22,3	1,79 : 1	
	L50004	43,4	24,8	1,75 : 1	
	L50006	37,8	21,1	1,79 : 1	
	L50446	44,0	23,4	1,88 : 1	
	L45114	43,1	22,8	1,89 : 1	
	L50005	43,9	22,9	1,92 : 1	
<i>Agriotherium insigne</i>	Montpellier ¹	40,0	22,5	1,78 : 1	1,79 : 1
	Montpellier ¹	38,0	21,5	1,79 : 1	
<i>Agriotherium palaeindicum</i>	GSI-D8 ²	42,7	21,3	2,00 : 1	2,00 : 1
<i>Indarctos punjabiensis</i>	GSI-D9 ²	39,6	21,1	1,88 : 1	1,88 : 1
<i>Indarctos atticus</i>	NMB-Sam31	41,6	22,2	1,87 : 1	1,90 : 1
	NMW-Sam1912/29 ³	39,3	20,4	1,93 : 1	
	Concud ⁴	42,4	22,2	1,91 : 1	
<i>Indarctos arctoides</i> ⁴	Westhofen	32,6	17,3	1,88 : 1	1,93 : 1
	Pfaffstetten	30,8	15,8	1,95 : 1	
	Montredon	35,7	18,3	1,95 : 1	
<i>Indarctos vireti</i> ⁴	Can Llobateres				2,01 : 1
	VP633	32,7	16,8	1,95 : 1	
	VP647	30,2	14,9	2,03 : 1	
	VP647	30,0	14,7	2,04 : 1	
	Can Purull				
	Type (<i>pontiensis</i>)	c. 34,5	17,3	1,99 : 1	
	Type	30,8	15,1	2,04 : 1	

¹ Viret 1939; ² Lydekker 1884; ³ Thenius 1959; ⁴ Crusafont & Kurtén 1976.

This is a significant difference, because once again a specimen of one genus is known which has the character of the other. An *Indarctos*-like post-metacone lengthening is one of the few features visible on the incomplete and badly restored M¹ of the Montpellier *A. insigne* specimen, NMB-MP549.

The 'primitive' M¹ of this remarkable specimen is yet another of its *Indarctos* 'characteristics', others being its relatively small size, double-rooted and transversely orientated P³, and double-cusped P⁴ protocone lobe. This specimen also has the P¹, M¹ and M² lower crowned than any of their counterparts in the Langebaanweg assemblage. However, it is identified with *Agriotherium* because its M² is of the *Agriotherium* type and distinct from that of all specimens referred to *Indarctos* (see below). Had the M² of this specimen not been preserved, it may well have been referred to *Indarctos*. Montpellier could therefore have erroneously acquired the distinction of being the only locality where *Indarctos* and *Agriotherium* occurred together. This imaginary situation is mentioned here to indicate the importance of NMB-MP549 as an *Indarctos*-*Agriotherium* 'intermediate', and to illustrate how easy it is to misidentify specimens belonging to late *Indarctos* and early *Agriotherium*. The possibility of similar confusion with certain Siwaliks specimens was mentioned above.

Before dealing with the next tooth in the dentition, another parallel between *Agriotherium* and *Thalarctos* is mentioned. The M¹ of the latter is relatively shorter and higher crowned than that of *U. arctos*, its 'structural' ancestor (Kurtén 1964). This also applies in the case of at least some species of *Arctodus* (Kurtén 1967).

The M₂ of *A. africanum*, and other *Agriotherium*, usually consists of two trigonid cusps side by side, flanked posteriorly by two similarly positioned talonid cusps. The M₂ of *Indarctos* differs only in having two lingual talonid cusps, and in being relatively longer and narrower. There are, however, *Agriotherium* specimens which are *Indarctos*-like in both these respects. The M₂ of the *A. palaeindicum* specimen GSI-D8 has two lingual talonid cusps, while vestiges of a second cusp are visible in the Langebaanweg specimens L54114/L46563 and L50007. The length:breadth ratios of the M₂'s of GSI-D8 and L45114/L46563 are comparable to those of *I. atticus* M₂'s (Table 18). By contrast, this ratio in the *I. punjabiensis* specimen GSI-D9 is the same as that of the mean of the *A. africanum* sample.

Curiously, the *A. africanum* M₂'s which are most *Indarctos*-like in respect of talonid cusps and proportions are those which are most specialized in terms of their trigonid development (see p. 27). Consequently, these specimens should not be considered as good *Indarctos*-*Agriotherium* intermediates. In addition, it could be argued that Pilgrim (1932) was incorrect in reversing Lydekker's (1884) identifications of GSI-D8 and D9 and that they, too, are not 'intermediates' in the sense claimed above. This may, indeed, be the case, but the fact remains that however these (and other) Siwaliks specimens are identified, they exhibit a combination of *Indarctos* and *Agriotherium* characters.

The dentitions of *Indarctos* and *Agriotherium* are perhaps most clearly

TABLE 18

Length : breadth ratios of *Indarctos* and *Agriotherium* M²'s.

TAXON	LOCALITY and/or NUMBER	LENGTH	BREADTH	L : B	MEANS
<i>Agriotherium africanum</i> .	{ L45062	28,6	c. 23,6	1,21 : 1	1,29 : 1
	L45062	29,3	24,0	1,22 : 1	
	L50004	32,3	26,0	1,24 : 1	
	L50003	30,4	24,1	1,26 : 1	
	L50007	28,8	21,9	1,32 : 1	
	L45114	32,6	23,5	1,39 : 1	
	L46563	34,0	24,3	1,40 : 1	
<i>Agriotherium insigne</i> .	Montpellier ¹	30,2	23,2	1,30 : 1	1,30 : 1
<i>Agriotherium palaeindicum</i> .	GSI-D8 ²	31,8	22,9	1,39 : 1	1,39 : 1
<i>Indarctos punjabiensis</i> .	GSI-D9 ²	29,2	22,6	1,29 : 1	1,29 : 1
<i>Indarctos atticus</i> .	NMB-Sam31	32,4	23,3	1,39 : 1	1,39 : 1
	NMW-Sam1912/29 ³	28,7	20,8	1,38 : 1	
<i>Indarctos arctoides</i> ⁴ .	Montredon	25,2	19,0	1,33 : 1	1,41 : 1
	Westhofen	25,2	17,4	1,45 : 1	
	Pfaffstetten	24,1	16,5	1,46 : 1	
<i>Indarctos vireti</i> ⁴ .	Can Llobateres				1,45 : 1
	VP633	25,0	17,2	1,45 : 1	
	VP640/1	26,1	18,0	1,45 : 1	
	{ VP647	23,7	16,2	1,46 : 1	
	{ VP647	23,6	16,2	1,46 : 1	
	Can Purull				
	Type	22,0	15,6	1,41 : 1	
	Type (<i>pontiensis</i>)	25,6	17,7	1,45 : 1	

¹ Viret 1939; ² Lydekker 1884; ³ Thenius 1959; ⁴ Crusafont & Kurtén 1976.

distinguished from one another by the fact that the M² of the latter lacks a talon, whereas in *Indarctos* this feature, although variably developed, is always present.

The postero-internal (talon) region of the *Agriotherium* M² is also variably developed, the Langebaanweg assemblage being useful in indicating the variation possible in a single population (Fig. 12). Of particular interest is the isolated M², L47698, in which there is a marked posterior projection of the postero-internal part of the tooth. This is here interpreted as the vestiges of the talon characteristically present in the M² of *Indarctos*. L47698 is remarkably similar to the M², GSI-D12, referred to *I. punjabiensis* by Lydekker (1884, fig. 6), and these two specimens represent an intermediate between the conditions typical of *Indarctos* and *Agriotherium*. The progressive shortening and broadening of M²'s in the *Indarctos*-*Agriotherium* lineage is indicated by the data in Table 19.

Erdbrink's (1953: 582) view that there is 'at best a beginning of a [M²] talon . . . in *A. insignis*' is here regarded as the reverse of the true situation. *A. insigne*, like *A. africanum*, sometimes has the vestiges of a M² talon.

As with M¹, the arrangement and morphology of the four principal cusps of M² in advanced *Indarctos* and *Agriotherium* are very similar. The paracones

TABLE 19

Length : breadth ratios of *Indarctos* and *Agriotherium* M²s.

TAXON	LOCALITY OF NUMBER	LENGTH	BREADTH	L : B	MEANS
<i>Agriotherium africanum</i>	L48577	25,4	30,2	0,84 : 1	0,91 : 1
	L48564	25,6	30,5	0,84 : 1	
	L41404	26,5	31,0	0,85 : 1	
	{ L45062	26,5	30,2	0,87 : 1	
	{ L45062	26,4	29,9	0,88 : 1	
	{ L45137	29,3	31,5	0,93 : 1	
	{ L45137	29,5	31,4	0,94 : 1	
	L47242	25,8	25,9	1,00 : 1	
	L47698	31,1	30,1	1,03 : 1	
<i>Agriotherium insigne</i>	NMB-MP549	25,2	28,3	0,89 : 1	0,96 : 1
	Type ¹	27,4	26,5	1,03 : 1	
<i>Indarctos punjabiensis</i>	GSI-D12 ²	28,2	26,7	1,06 : 1	1,06 : 1
<i>Indarctos atticus</i>	NMW-Sam1912/29 ³	30,0	26,5	1,13 : 1	1,21 : 1
	NMB-Sam31	33,4	26,1	1,28 : 1	
<i>Indarctos arctoides</i>	Montredon ⁴	31,0	24,0	1,29 : 1	1,34 : 1
	Montredon ⁴	29,3	20,5	1,43 : 1	
	Orignac ⁴	28,2	22,0	1,28 : 1	
	Gau-Weinheim ⁵	25,1	18,3	1,37 : 1	
<i>Indarctos vireti</i>	VP633 ⁴	27,9	19,0	1,47 : 1	1,43 : 1
	VP646 ⁴	27,3	19,7	1,39 : 1	

¹ Frick 1926; ² Lydekker 1884; ³ Thenius 1959; ⁴ Crusafont & Kurtén 1976; ⁵ Tobien 1955.

and metacones are conical, with distinct anterior and posterior keels, the protocone is ridge-like, and, with the small hypocone, is lower than the buccal cusps.

The M²s of *Indarctos* and *Agriotherium* illustrate very clearly a progressive development from *I. vireti*, through *I. arctoides*, *I. atticus*, *I. punjabiensis* to *Agriotherium*, with *A. africanum* taken as an example of its genus (Fig. 37). The recorded M²s of advanced North American *Indarctos* all have well-developed talons, that of the *I. cf. oregonensis* specimen recorded by Merriam & Stock (1925) being the most prominent. It is, however, from the same deposits as another *I. oregonensis* M², which is a larger tooth but with a relatively smaller talon (Merriam *et al.* 1925). The latter is here interpreted as belonging to a male, while the smaller specimen with the larger talon belongs to a female.

This raises the possibility that the teeth of female *Indarctos* and *Agriotherium* tend to be more 'primitive' than those of the larger males. This explanation applies in the case of the 'primitive' *A. insigne* specimen, NMB-MP549, discussed earlier, which represents a small individual, apparently a female. Another example is the *A. africanum* M₁ with the vestigial metaconid, L50006. The female *I. cf. oregonensis* is also 'primitive' compared with other North American *Indarctos* in having a relatively small P⁴ parastyle and a relatively elongated M¹. It does not, however, have a double-cusped P⁴ protocone lobe. This, together with the fact that NMB-MP549 does not have a talon on M²,

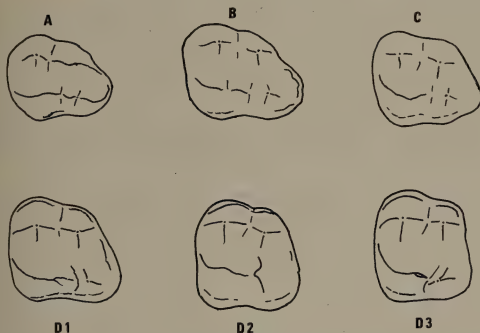


Fig. 37. M^2 s. A. *Indarctos arctoides* (after Helbing 1932, fig. 7). B. *Indarctos atticus* (after Helbing 1932, fig. 1). C. *Indarctos punjabiensis* (after Lydekker 1884, fig. 6). D. Langebaanweg *Agriotherium* (D1—LA7698; D2—LA5137; D3—LA1404).

indicates that females were not necessarily 'primitive' in all respects. Nevertheless, since increasing size was a characteristic of the *Indarctos*-*Agriotherium* lineage, and consequently large size was itself an 'advanced' character, it is to be expected that larger individuals would also be 'advanced' in other respects, and vice versa. This is a further indication that allowance must be made for appreciable variation in characters in studies on *Indarctos* and *Agriotherium*. The fact that known North American *Indarctos* M^2 s appear more 'primitive' than the *I. punjabiensis* specimen, GSI-D12, does not necessarily mean that they must be older.

There is other evidence to support this opinion. Once again there is a parallel between *Agriotherium* and *Thalarcos*, since the latter also has the M^2 talon reduced, and it may sometimes even be absent. The study by Kurtén (1964) has shown that there is considerable variation in *Thalarcos* in this respect even within a single population. Particularly remarkable is a specimen in which the right M^2 talon is reduced, while that of the left M^2 is completely absent (Kurtén 1964: 17, pl. 4A). Such examples are exceptional, but presumably if samples of *Indarctos* as large as Kurtén's *Thalarcos* sample ($n = 113$) were available, similar specimens may be found. This suggests that undue reliance may have been placed on the value of the M^2 talon as a distinguishing characteristic of *Indarctos*.

The M_3 of *Indarctos* and *Agriotherium* is less commonly represented than other posterior cheek teeth, evidently because it is single-rooted and easily

separated from the mandible. It is nevertheless clear that this tooth was reduced in length in the *Indarctos-Agriotherium* lineage to a degree comparable to that of M^2 . In *I. vireti* the M_3 is markedly elongated anteroposteriorly and has a pronounced posterior tapering (Crusafont & Kurtén 1976). The M_3 of *I. atticus* is similar, but is less elongated, while that of *Agriotherium* is usually only as long as it is broad. The latter, however, is still *Indarctos*-like in having a pronounced posterior tapering. The *A. africanum* M_3 , L50981, is very like those of the Vienna and Basel *I. atticus* specimens (Thenius 1959; Helbing 1932) in shape.

The reduction of M_3 is another development shared by *Agriotherium* and *Thalarcos*.

Although mention has been made of differences in proportions in certain of the posterior cheek teeth discussed above, this matter warrants more detailed attention, since these differences are directly related to changes in tooth morphology and are as significant from a phylogenetic point of view. In addition, metrical data have the advantage of being easily represented diagrammatically and can thus give a visual impression of certain evolutionary changes in the hypothetical *Ursavus-Indarctos-Agriotherium* lineage. Five Old World species were selected to represent successive stages in this lineage. They are *Ursavus primaevus*, *I. vireti*, *I. arctoides*, *I. atticus*, and *A. africanum*. Individual species do not necessarily represent the stock from which the next in the series was derived, but are simply structurally suited to such a role. The lengths and breadths of their posterior cheek teeth are plotted in Figures 38-40.

It is clear from these figures that *U. primaevus* is in an isolated position, whereas there are similarities between *I. vireti* and *I. arctoides* on the one hand,

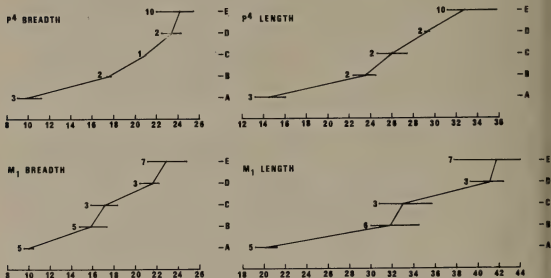


Fig. 38. Lengths and breadths of P^4 and M_1 . A. *Ursavus primaevus*. B. *Indarctos vireti*. C. *I. arctoides*. D. *I. atticus*. E. *Agriotherium africanum*. Sample sizes, ranges and means are indicated. Data from Crusafont & Kurtén (1976), Thenius (1959) and this report.

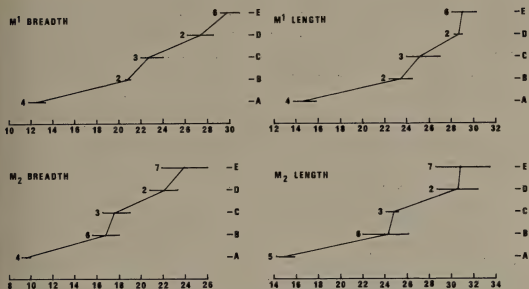


Fig. 39. Lengths and breadths of M^1 and M_2 of some Ursidae, (see Fig. 38 for key).

and *I. atticus* and *A. africanum* on the other. The isolated position of *U. primaevus* is not surprising since it is a contemporary of *I. vireti* (Crusafont & Kurtén 1976), and its phylogenetic connection with the *Indarctos-Agriotherium* lineage must be indirect. The fact that this lineage is divisible into two parts on the basis of cheek tooth size (and other evidence) is significant. The first is comprised of earlier, smaller and more primitive forms (i.e. *I. vireti*-*I. arctoides*), and the second of later, larger and more advanced forms (i.e. *I. atticus*-*A. africanum*).

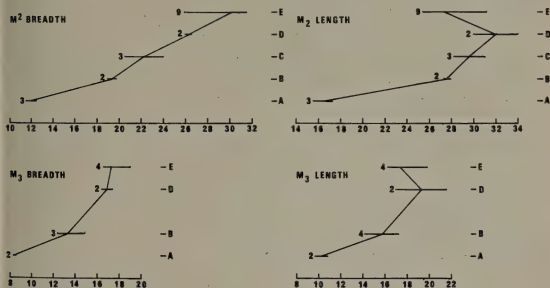


Fig. 40. Lengths and breadths of M^2 and M_3 of some Ursidae, (see Fig. 38 for key).

It is only in the last segment of the lineage that there are deviations from otherwise general trends in the lineage as a whole. The most obvious of these general trends was the increasing breadth of the posterior cheek teeth. This was probably more or less in proportion to the overall size increase of the taxa concerned. However, the situation in respect of the lengths of these teeth is more complex.

Only in the case of P^4 was there a tendency to increase length throughout the *Ursavus-Indarctos-Agriotherium* lineage. This is also a reflection of the increasing size of successive members of the lineage. In addition, it may be interpreted as indicating the increasing functional importance of the principal shearing tooth in the upper dentition, with the increased lengths of P^4 in the last stage of the lineage (i.e. *I. atticus-A. africanum*) being largely due to the development of the parastyle. It might be expected that there would have been a corresponding increase in the length of the lower carnassial. The fact that there is a barely perceptible increase in the mean length of the *A. africanum* M_1 over that of *I. atticus* may simply be due to the composite nature of this tooth, the increased length of the shearing element (i.e. the trigonid) being obscured by the reduction of the talonid.

By contrast, in the case of M^2 and M_3 the lengthening trend evident in most of the lineage is reversed in the *I. atticus-A. africanum* segment. This is a manifestation of the reduced importance of the crushing function of the most posterior cheek teeth in the last stage of the lineage.

The situation in respect of the lengths of the intermediate teeth, M^1 and M_2 , was itself intermediate, with lengths remaining static once the *I. atticus* stage was reached.

The overall impression gained from the study of the morphology and dimensions of the teeth of successive members of the *Ursavus-Indarctos-Agriotherium* lineage is that this lineage can be separated into two parts. Up to the *I. atticus* stage the taxa concerned were generalized 'omnivorous' ursids, but thereafter there were modifications of both tooth morphology and proportions being manifested which indicate adaptation to a more carnivorous diet. It may thus be more appropriate to think of 'advanced *Indarctos*' as being 'primitive *Agriotherium*'.

Since the transition from *Indarctos* to *Agriotherium* was gradual in the sense that there are specimens which exhibit 'characteristics' of both genera, it is far from obvious on what grounds the distinction between these genera is to be made. Earlier attempts to find distinguishing characters are now seen to have been inadequate. For example, lists of such characters given by Pilgrim (1932: 42) and Tobien (1955: 14) can be misleading and should be used with caution, if they are to be used at all. The formulation of mutually exclusive diagnoses for these genera has become difficult, if not impossible. There would, of course, be no problem if these diagnoses were to be based on a primitive *Indarctos*, such as *I. vireti*, and any of the species presently identified with *Agriotherium*. However, when all recorded intermediate forms are taken into

account, the diagnoses break down under a welter of qualifying statements. The situation could only become more confused if all the *Indarctos* and *Agriotherium* assemblages from the critical 5–8 Ma period were as large, or larger, than that from Langebaanweg. Even if this is never the case, the Langebaanweg assemblage has clearly shown that agriotheriines are as variable as other ursids, and consequently there can no longer be complacency about supposed 'characteristics' of individual representatives of this group.

This situation is here interpreted as indicating an ancestor–descendant relationship between *Indarctos* and *Agriotherium* beyond all reasonable doubt. In concluding his study of the Florida *Indarctos*, Wolff (1978: 11) stated that there are 'several cranial features [which] may indicate a relatively closer relationship between *Ailuropoda* and *Indarctos* than with other bears, although other possibilities exist'. In the light of the preceding discussion and the fact that the Florida *Indarctos* skull is even more like that of *A. africanum* than *Ailuropoda*, the 'other possibilities' must certainly include *Agriotherium*. The similarities between the skulls of advanced *Indarctos*, particularly the Florida specimen, and *Agriotherium* are so great that it is inconceivable that they are only distantly related. Wolff's concluding remarks refer specifically to 'great enlargement of the cheek teeth', 'expansions of the zygomatic arches and sagittal crests', and the 'absence of the alisphenoid canal' as shared characters indicative of the 'close relationship' between *Indarctos* and *Ailuropoda*. The fact that *Indarctos* and *Agriotherium* also share them is equally significant, especially taken in conjunction with all the other evidence cited above.

It seems superfluous at this stage to consider alternative theories on the origin of *Agriotherium*, but one is mentioned here since it apparently still has some support.

The fact that *Agriotherium* and the Hemicyoninae have a premasseteric fossa on the mandible in common has contributed to the belief that they are closely related (e.g. Frick 1926). There is also a superficial similarity between the dentitions of *Agriotherium* and hemicyonines, and both are supposedly canid-like, rather than ursine-like. This is indeed so in the case of hemicyonines, but in terms of the arrangement, morphology and size of individual cusps, the teeth of *Agriotherium* are far more like those of advanced *Indarctos* than any hemicyonine. It could, of course, be argued that the rather generalized hemicyonines are structurally suitable in both cranial and postcranial characters to be ancestral to *Agriotherium*. This more tenuous hypothesis is considered less likely than the alternative suggested here.

It was indicated earlier that the known temporal ranges of *Indarctos* and *Agriotherium* are in accord with the theory that the latter was derived from the former. In the case of the Hemicyoninae–*Agriotherium* alternative the situation is much less convincing because of an apparent, or actual, gap between the recorded histories of the taxa concerned.

In Europe *Agriotherium* is first recorded from the Ruscinian, whereas hemicyonines were extinct by the end of the Vindobonian (Table 20). This

TABLE 20

The occurrences of Hemicyoninae and *Agriotherium* in Europe.

TAXON	LOCALITY	MAMMAL AGE ¹	MEIN ZONE ²	APPROX. AGE IN m.y. ¹
<i>Agriotherium insigne</i>	Montpellier	Ruscinian	14	5
—	—	Turolian	11–13	—
—	—	Vallesian	9–10	—
<i>Hemicyon sansaniensis</i> , <i>Hemicyon goeriachensis</i> etc. ³	Wintershof- West, Sansan, Göriach, La Grive-St-Alban, Steinheim etc ³	Burdigalian to Vindobonian	3–8	13–18

¹ Van Couvering 1972, Fahlbusch 1976; ² Mein 1975, Fahlbusch 1976; ³ Heizmann 1973.

means that there was a period of about 8 m.y. for which no possible intermediate between hemicyonines and *Agriotherium* is known in Europe. Much the same applies in Asia and North America. It is unlikely that this could be due to a defective fossil record, since the period in question covers the Vallesian and Turolian (and their equivalents), of which the faunas are moderately to very well known. It is possible that the Hemicyoninae–*Agriotherium* transition took place in Africa, where 5–13 Ma faunas are poorly known, but negative evidence is hardly convincing support for a theory.

It is much more likely that the characters Hemicyoninae and *Agriotherium* have in common are due to convergent evolution. Parallel and convergent evolution often complicate studies of relationships, and the Ursidae are a group where this complication definitely exists. Early in the history of the Ursidae, the Amphicyoninae and Hemicyoninae evolved along parallel lines, while later the same applied to the Ursinae and Tremarctinae. *Agriotherium* is of particular interest in this connection, since not only is it intermediate in age between amphicyonines/hemicyonines and ursines/tremarctines, but it has in certain respects paralleled members of both sets of subfamilies.

The superficial similarities between *Agriotherium* and large amphicyonines and hemicyonines (e.g. *Amphicyon major*, *Dinocyon thenardi*) are striking enough to suggest that these animals were ecological vicars. On the other hand, *Agriotherium*, *A. major* and *D. thenardi* (and better known hemicyonines) also differ from one another in certain respects, which can be explained by their having evolved at different times from different ancestors.

Amongst the Ursinae, *Thalarcos* has now been mentioned several times as having evolved characters comparable to some in *Agriotherium*. In this instance there is no possibility of the shared characteristics being due to a close relationship. They are simply explained by the fact that both *Agriotherium* and *Thalarcos* are essentially carnivorous forms which evolved from omnivorous ancestors (Hendey 1972: 122). The relationship between *Thalarcos* and the *Ursus arctos* group has been well documented (Thenius 1953; Kurtén 1964),

and is here regarded as a parallel of the relationship between advanced *Indarctos* and *Agriotherium*. A more detailed search for parallelisms between these two sets of taxa may well be worth while. The obvious differences between *Agriotherium* and *Thalarctos* are not unexpected, since their ancestral forms are markedly different from one another. In addition, *Thalarctos* has as yet had a relatively brief history compared with that of *Agriotherium*. Given time it would no doubt become increasingly distinct from *U. arctos*, and perhaps become even more *Agriotherium*-like.

Agriotherium and advanced *Indarctos* are also paralleled in some respects by tremarctines, especially the large extinct species. For example, several references have been made above to similarities between the skull and skeleton of *A. africanum* and *Arctodus simus*. Merriam & Stock (1925: 5) found that there are certain characters 'in which *Tremarctos* and [*Arctodus*] show distinctly closer affinity to [*Agriotherium*] and its allies of the Pliocene than is seen in Pleistocene and Recent bears of the genus *Ursus*'. Others have thought this significant. For example, Erdbrink (1953) suggested that *Tremarctos* was closely related to the ursines, while the larger tremarctines were derived from advanced *Indarctos*. Kurtén (1966: 7) disagreed, and concluded that although the 'earlier history of *Arctodus* is poorly documented . . . there can be little doubt that it is a tremarctine, and not a member of the Agriotheriinae'.

The *Indarctos*-*Agriotherium* lineage was but one of several evolutionary developments amongst the Ursidae during the latter part of their history. As indicated above, it was a development which paralleled that undergone earlier by large amphicyonines and hemicyonines, but it, too, was ultimately unsuccessful and by the end of the Tertiary *Agriotherium* was on the verge of extinction, if not already extinct. It had no descendants.

Other later ursid lineages, however, were more successful. This applies particularly in the case of the one which gave rise to the Ursinae, which underwent a spectacular radiation beginning in the Pliocene. As with *Indarctos*-*Agriotherium*, the Ursinae also stemmed from *Ursavus*, and Thenius (1977 and earlier papers) has suggested *U. ehrenbergi* as the likely ancestral form.

The Tremarctinae were less successful than the Ursinae, having been confined to the Americas, and eventually being supplanted in North America by the Ursinae (Kurtén 1966, 1967). Their origins were recently considered by Thenius (1976), who suggested that they, too, stemmed from an *Ursavus*. Unfortunately, little is known of early tremarctines, but no doubt more will yet be learnt of the origins and early history of this group.

The origin of the giant panda, *Ailuropoda melanoleuca*, has long been a controversial issue. The earlier views that *Ailuropoda* is an ursid and not a procyonid, and that it had an agriotheriine ancestor (Hendey 1972), are maintained here, although it now appears that it may have stemmed from *Ursavus* and not *Indarctos* as previously suggested.

As indicated earlier, the skulls of *Ailuropoda* and advanced *Indarctos* have many characters in common which suggest that they are more closely related

to one another than to other bears. However, the latter had already undergone specializations in the direction of *Agriotherium* which render it structurally unsuitable as a stem form for *Ailuropoda*. For example, advanced *Indarctos* has reduced anterior premolars, while those of *Ailuropoda* are unusually large for an ursid. This objection does not apply in the case of earlier, unspecialized *Indarctos* (see Hendey 1972, table 1), but since such species have much in common with *Ursavus*, the latter must also be taken into account when considering the origin of *Ailuropoda*.

One of the less well-known species of *Ursavus* is *U. depereti* of the European Turolian, which is in some respects atypical of the genus (see Heizmann 1973). This applies particularly to the P⁴, and it is the unusual characteristics of this tooth which suggest that *U. depereti* may have a direct phylogenetic connection with *Ailuropoda*.

Casts of upper teeth of *U. depereti* from Soblay in France were recently examined in the Naturhistorisches Museum, Basel. The originals are in Lyon and were described by Viret (1949) and Viret & Mazenot (1949). Two P⁴'s are represented and they are remarkable for two reasons. Firstly, unlike the P⁴'s in other *Ursavus* species, the Soblay specimens have large parastyles. This cusp is proportionately even larger than those in advanced *Indarctos* and in *Agriotherium*, in which the parastyles are overshadowed by large and high-crowned paracones. The large parastyle and relatively low-crowned paracone of *U. depereti* are reminiscent of the situation in *Ailuropoda*, and differ from that in all other ursids. Secondly, the *U. depereti* P⁴ has an enlarged, double-cusped protocone lobe, which differs from that in *Indarctos* and *Agriotherium* in being more anteroposteriorly elongated and regular in occlusal outline. In addition, in the Soblay specimen, AA52 (Viret & Mazenot 1949, pl. 1 (fig. 6)), both cusps are ridge-like rather than pointed and are of more or less equal size. In all these respects the *U. depereti* P⁴ protocone lobe is *Ailuropoda*-like, and once again it differs from that in all other ursids.

The M¹ and M² of *U. depereti* are also basically similar in morphology to their counterparts in *Ailuropoda*. However, the upper molars are also similar to those of other *Ursavus* species and *Indarctos*, and are thus less significant in indicating a relationship with *Ailuropoda*. A possibly important characteristic of the M² figured by Viret & Mazenot (1949, pl. 1 (fig. 4)) is the rugose enamel of the occlusal surface, which could foreshadow the 'richly tuberculate' condition of the *Ailuropoda* M² (Davis 1964: 127).

The M₁ and M₂ of *U. depereti* also have the basic morphology characteristic of other *Ursavus* and *Indarctos*, although the M₁ is distinct, and more *Ailuropoda*-like, in having the metaconid more anteriorly situated (Schlosser 1902, pl. 2 (figs 20, 23)).

Slender though the evidence may be, *U. depereti* appears to be structurally better suited than any other recorded fossil ursid to fill the role of ancestor to *Ailuropoda*. In addition, it is also temporarily and geographically well suited to this role since it is from the continent on which the early evolution of living

bears was centred and it dates from a period when the radiation of later bears was just beginning. The absence of any intermediate forms may simply be due to the relatively poor Pliocene record in Asia, the continent to which *Ailuropoda melanoleuca* is confined (Chorn & Hoffmann 1978). Relevant fossils of Pliocene age, as well as better knowledge of *U. depereti*, are required to test this theory of *Ailuropoda* origins.

While the ultimate origins of both *Ailuropoda* and the *Indarctos*-*Agriotherium* lineage are uncertain, it is evident that these genera are more closely related to one another than to the Ursinae and Tremarctinae.

The radiation of the Ursidae, like that of some other mammalian families, was thus characterized by repetitious evolutionary developments, and the correct identification of relationships requires careful study of the fossil record. Ignorance of the details of this record may well lead to misinterpretation of the significance of similar, but independently evolved characteristics in ursid taxa. Kurtén (1967: 5) has found, for example, the analogy between European Miocene *Indarctos* and North American Pleistocene *Arctodus* to be 'truly astonishing and an example of the *déjà vu* experiences so familiar to the student of fossil bears'.

The relationships suggested here are indicated in Figure 41. The named late Tertiary species are all from Europe and consequently the European subdivisions of this period are used.

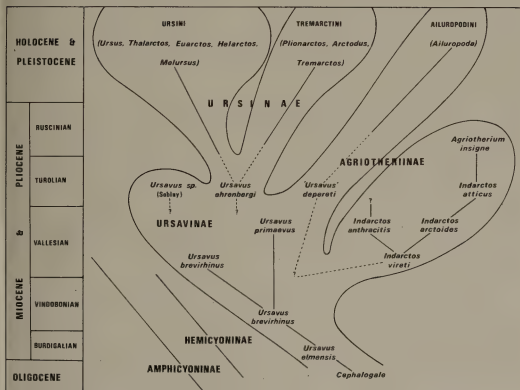


Fig. 41. Suggested relationships of some Ursidae.

NOMENCLATURE

The suprageneric classification of the Ursidae adopted here (Table 21) is a modification of an arrangement suggested earlier (Hendey 1972: 119), and is based on the phylogenetic relationships indicated in Figure 41.

TABLE 21
A classification of the Ursidae.

SUBFAMILY	TRIBE	GENERA, SPECIES
Amphicyoninae	Not subdivided	† <i>Amphicyon</i> , † <i>Cynelos</i> and †others
Hemicyoninae	Not subdivided	† <i>Hemicyon</i> , † <i>Dinocyon</i> and †others
Ursavinae	Not subdivided	† <i>Ursavus</i>
Agriotheriinae	Agriotheriini	† <i>Indarctos</i> , † <i>Agriotherium</i>
	Ailuropodini	† <i>'Ursavus' depereti</i> , <i>Ailuropoda</i>
Ursinae	Tremarctini	† <i>Plionarctos</i> , † <i>Arctodus</i> , <i>Tremarctos</i>
	Ursini	<i>Ursus</i> , <i>Thalarchos</i> , <i>Euarctos</i> , <i>Helarctos</i> , <i>Melursus</i>

† = extinct

In preceding sections of this report the generally accepted practice of allowing the ursines and tremarctines subfamilial status has been followed. With this as a precedent, it follows that the agriotheriines and *Ailuropoda* each warrant similar status. Some of those who have included *Ailuropoda* in the Ursidae have, indeed, placed it in a separate subfamily (e.g. Pilgrim 1932). Similarly, the agriotheriines have been widely recognized as a valid subfamily (e.g. Kurtén 1966).

A disadvantage with this arrangement is that it does not indicate the apparently close relationships between the ursines and tremarctines on the one hand (Kurtén 1966, 1967; Thenius 1976), and the agriotheriines and *Ailuropoda* on the other (Hendey 1972; Wolff 1978; this report). This problem is overcome by reducing the status of the four subfamilies to tribes, and then separating them into two subfamilies, namely, the Agriotheriinae (Agriotheriini and Ailuropodini) and the Ursinae (Ursini and Tremarctini). Except for the position of the Tremarctini, this was the arrangement suggested earlier (Hendey 1972), and for which there has been some support (e.g. Chorn & Hoffmann 1978).

There is also a difference now in the taxa constituting the Agriotheriinae.

Firstly, in the classification suggested here, *Ursavus depereti* is included in the Ailuropodini, since it is regarded as the likely ancestor of *Ailuropoda*. This means that it can no longer be referred to *Ursavus*, but must either be given a new generic name, or be referred to *Ailuropoda* itself. The latter course is favoured here, but in view of the uncertainties still surrounding this species neither of these alternatives is followed, and the doubtful generic identity of '*Ursavus' depereti* is indicated by quotation marks.

Secondly, if the Ursini, Tremarctini and Ailuropodini did, indeed, stem from the *Ursavus* group and are valid tribes, then the *Indarctos*-*Agriotherium* group of the Agriotheriini must be given the same status. This means that *Ursavus*, which is generally regarded as an agriotheriine (e.g. Kurtén 1966; Hendeby 1972), has to be excluded from the tribe.

The various species of *Ursavus*, excluding '*Ursavus*' *depereti*, are accordingly placed in a new subfamily, the Ursavinae. Since this subfamily is not established on the same criteria as the others, it constitutes an unsatisfactory element in the classification as a whole. When their relationships are better understood, it may be possible to assign the species of *Ursavus* to other tribes, just as '*Ursavus*' *depereti* has been assigned to the Ailuropodini. The need for this additional subfamily will then fall away.

The classification of more primitive ursids, or ursid-like carnivores, namely, the hemicyonines and amphicyonines, was not investigated since they are largely irrelevant to the present study. They are mentioned here for the sake of completeness, but the conclusions regarding their status are tentative.

The Hemicyoninae are generally regarded as an early off-shoot of primitive ursid stock (probably *Cephalogale*—see Erdbrink 1953, fig. 61; Hendeby 1972, fig. 1), and they are here included in the Ursidae.

The connection between the Amphicyoninae and later ursids is more remote, and the classification of this group is more controversial. They have been variously classified as a separate family (e.g. Hunt 1972), a subfamily of the Canidae (e.g. Kuss 1965), and as an ursid subfamily (e.g. Ginsburg 1977). The latter course is followed here.

The nomenclature of the species constituting the Agriotheriini is a far more problematical matter than the suprageneric classification of the Ursidae.

The conclusion that *Agriotherium* is directly descended from *Indarctos* with certain specimens exhibiting a combination of 'characteristics' of both genera, raises the possibility that they are congeneric, with *Agriotherium* the senior synonym. This situation had been foreseen even before *Indarctos* became well established in the literature (Pilgrim 1914; Merriam *et al.* 1916). It can be considered in relation to a similar situation involving the brown and polar bears.

Ewer (1973) and Van Valen (1978) have recently discussed the relative merits of opposing opinions on the generic identity of the polar bear. According to one widely held opinion the polar bear and brown bear are congeneric (i.e. both belong to the genus *Ursus*), while the opposing view is that the polar bear represents a separate genus (i.e. *Thalarctos*). Ewer and Van Valen favoured the latter alternative, a view which is supported here. A problem with this arrangement is that by one widely accepted criterion *Thalarctos* does not merit separate generic status. *Thalarctos maritimus* and *Ursus arctos* are known to produce fertile hybrids (see Van Gelder 1977). Van Valen (1978: 292) dismissed this objection in the grounds that 'lack of intersterility *per se*' is of 'low evolutionary importance' a fact for which Vrba (1979) has found supporting evidence amongst the Bovidae.

It is clear from their habitats and habits that *Thalarcos* and *U. arctos* are set on distinct evolutionary paths, and that given time they may well warrant generic separation by any standards. It is fortuitous that at present their divergence is not far advanced, although there is no doubt that this divergence does, in fact, exist. There will always be a problem in classifying species, both living and extinct, which are on separate lineages, but which are still close to a common ancestor. In instances where divergence is certain, and in the case of the brown and polar bears it is, then classification by 'clade' rather than 'grade' is preferable.

As indicated earlier, *Thalarcos* and *Agriotherium* are similar in the sense that both are essentially carnivorous forms derived from omnivorous ancestors. There is an apparent difference, however, in the evolutionary histories of these two genera. In the case of *Thalarcos* there was a divergence from the *U. arctos* group after which two lineages evolved independently, one with essentially carnivorous elements, and the other continuing with essentially omnivorous ones. In the case of *Indarctos*-*Agriotherium* it has been suggested above that the essentially omnivorous ancestor gradually adapted to give rise to the more carnivorous descendant forms and did not itself continue to exist as a separate entity. In other words, successive members of what may be regarded as a single lineage adapted their habits in response to a gradually changing environment (see p. 70).

This may, of course, be a misinterpretation of the fossil record and there may have been a dichotomy during the history of *Indarctos*-*Agriotherium* similar to that of *U. arctos*-*Thalarcos*. For example, Crusafont & Kurtén (1976) may be correct in their interpretation of the early history of *Indarctos*, and *I. vireti* may have given rise to both *I. arctoides* and the more *Agriotherium*-like *I. atticus*. According to this interpretation *I. vireti*-*I. arctoides* would be an equivalent of the *U. arctos* lineage, while *I. atticus* was the counterpart of *Thalarcos*. The nomenclatural implication is that *I. atticus* and other later *Indarctos* should be referred instead to *Agriotherium*, leaving only *I. vireti*, *I. arctoides* and the aberrant *I. anthracitis* as representatives of *Indarctos*. This arrangement is supported by the earlier suggestion that those species referred to throughout this report as 'advanced *Indarctos*', could as well be regarded as 'primitive *Agriotherium*'. A minor difficulty which arises is that *Indarctos* would have to be replaced by another name, because the genotype (*I. salmontanus*) would then be identified as an *Agriotherium*.

It could also be argued that since *I. vireti* is readily distinguishable from contemporary *Ursavus*, the evolutionary changes which were to culminate in *Agriotherium* were already being manifested early in the Vallesian. Thus *I. vireti* relative to contemporary *Ursavus* was the counterpart of the present-day situation involving *Thalarcos* and *U. arctos*. According to this interpretation all species presently identified with *Indarctos* should be referred instead to *Agriotherium*.

Both the above arrangements are less arbitrary than the existing one in

which it is only the most advanced agriotheriines which are referred to *Agriotherium*. This is unsatisfactory because it does not reflect the realities of the situation. Nevertheless, no changes in this arrangement are proposed here. Undescribed *Indarctos* and *Agriotherium* material from Asia and North America is available, and a decision regarding the status of these genera is best left until it, too, can be taken into account.

The same applies in the case of nomenclature at the species level, although some changes which reflect opinions on relationships are proposed here.

An appropriate starting point is with the European species, since they are amongst the best known and they represent the primary group from which agriotheriines elsewhere evolved. Four late Miocene species are recognized as valid. They are *I. vireti*, *I. arctoides*, *I. atticus* and *I. anthracitis*. *I. atticus* was apparently the first species to spread into Asia. *I. maraghanus* (De Mecquenem 1925) and *I. lagrelii* (Zdansky 1924) were apparently broadly contemporaneous with *I. atticus* and are here regarded as junior synonyms of this species.

The situation in respect of Siwaliks species is more problematical. The identifications of Pilgrim (1932), although regarded as unsatisfactory in some respects, are accepted here. Various possibilities will have to be considered in a revision of the Siwaliks material. For example, *I. punjabiensis* and *I. salmontanus* may represent a single species which is conspecific with *I. atticus*. Alternatively this species, or perhaps only *I. punjabiensis*, may be more advanced. The possibility that advanced Siwaliks *Indarctos* is conspecific with *A. palaeindicum* will also have to be considered. *A. sivalense* will be mentioned below.

Advanced *Indarctos* is also represented in Africa (Sahabi—see p. 73), and in North America, where material has been identified as *I. oregonensis* (e.g. Dalquest 1969), *I. nevadensis* (MacDonald 1959), or not identified as to species (e.g. Wolff 1978). There is no reason to believe that recorded North American *Indarctos* represents more than one species. Whether it should be identified as *I. oregonensis*, or referred to one of the Old World species, is not certain. The North American species was an immigrant from the Old World during the Hemphillian (Repenning 1967), and must, therefore, be closely related to a contemporary Asian species. It is here regarded as definitely distinct from *I. atticus*, but if *I. punjabiensis* is a valid species, it might be conspecific with, and the senior synonym of *I. oregonensis*.

Largely because of the uncertainties surrounding the Siwaliks species, *I. oregonensis* is here retained as a distinct species. In addition, the possibility was mentioned earlier that in certain respects North American *Indarctos* evolved independently of, and at a more rapid rate than its counterparts in Europe and Africa (see p. 82). If this were a development peculiar to North America, rather than both Asia and North America, then it would be another reason for recognizing *I. oregonensis* as a distinct species.

The situation in respect of recorded species of *Agriotherium* is complex, although the final solution with these species may be very simple. This solution, which is not advocated yet, is for all species of *Agriotherium* to be regarded as

junior synonyms of *A. sivalense*. Judged on the basis of the variation observed in the Langebaanweg *Agriotherium*, there may be no size or morphological grounds for recognizing more than one species of *Agriotherium*. However, it was decided to draw at least some distinctions on a geographical basis.

European *A. insigne*, which is here taken to include *A. intermedium* (Stach 1957), is tentatively regarded as valid. It was suggested earlier that African *Agriotherium* was an offshoot from the primary European lineage, and although *A. africanum* is almost indistinguishable from *A. insigne*, they are not regarded as conspecific, since the former is likely to be a descendant of north African *Indarctos* and was thus probably only indirectly related to European *A. insigne*.

There are some distinctive features in the dentitions of recorded *A. insigne* and *A. africanum* specimens which suggest that their phylogenetic connection may, indeed, have been indirect. For example, the European *A. insigne* specimen, NMB-MP549, has a double-rooted P³, a condition unknown in the Langebaanweg sample. On the other hand, no European specimen is known which has an 'intermediate cusp' on the P⁴ protocone lobe or a vestigial M₁ metaconid, while none is known to lack the anterolingual cusp of M₂. The possibility that European and African *Agriotherium* evolved independently will be discussed again below.

The situation in respect of *Agriotherium* in Asia and North America is similar to that with the *Indarctos* of these continents. *A. sivalense* is definitely a valid species, while *A. palaeindicum* is only tentatively regarded as such. Chinese *Agriotherium* is probably referable to *A. sivalense*. There is almost certainly only one species of *Agriotherium* represented in North America, and this may also be referable to *A. sivalense*. However, the North American species name which has priority, *A. schneideri* (Sellards 1916), is provisionally retained.

It has generally been assumed that North American *Agriotherium*, like *Indarctos*, was an immigrant from Asia (e.g. Repenning 1967). This is clearly a simple and logical interpretation of a situation where one genus supersedes another closely related one on a continent known to have received immigrants during the period in question. However, this is not the only interpretation possible. The fact that North American *Indarctos* includes some of the most *Agriotherium*-like specimens known suggests that the *Indarctos*-*Agriotherium* transition may have taken place in North America. If this were so then either the subsequent dispersal of *Agriotherium* started in North America, or *Agriotherium* evolved independently from advanced *Indarctos* in North America as well as in Europe and Africa.

The former alternative is unlikely in view of what is known of the Old World history of agriotheriines, whereas the independent evolution theory is a distinct possibility. This alternative appears to be implausible only in that it involves the polyphyletic origin of one genus as it is presently conceived. If, as indicated earlier, 'advanced *Indarctos*' is interpreted instead as 'primitive *Agriotherium*', it would mean that the *Indarctos*-*Agriotherium* transition took place once only (probably in Europe), and that once this evolutionary course

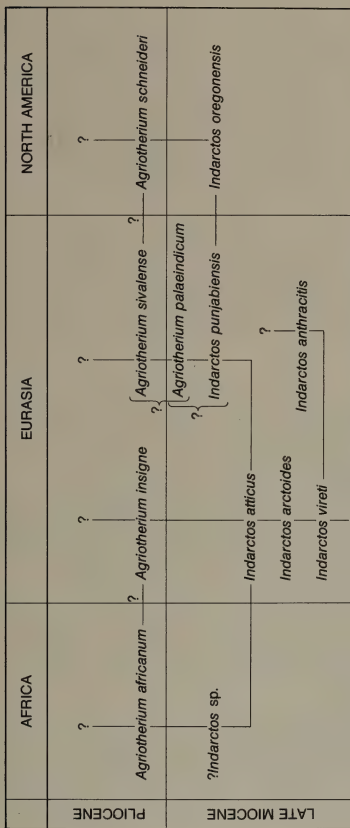


Fig. 42. A tentative arrangement of Agriotheriini in time and space.

had been set the development of *Agriotherium* (*sensu stricto*) could take place irrespective of the geographical location of the populations concerned.

Thus European *A. insigne* may have been descended from '*I.*' *atticus*, *A. africanum* from the north African *Indarctos*-like agriotheriine, *A. sivalense* from the '*I.*' *punjabiensis*/*A. palaeindicum* complex in Asia, while in North America '*I.*' *oregonensis* was ancestral to *A. schneideri*. It is nevertheless clear that there was a close connection between advanced agriotheriines in Europe and Africa on the one hand, and in Asia and North America on the other, and the above scenario may therefore be unrealistic. Instead *A. insigne* and *A. africanum* may share a common ancestor and be conspecific, while the same may apply to *A. sivalense* and *A. schneideri*. These alternatives are indicated in Figure 42. The possibility that all *Agriotherium* (*sensu stricto*) evolved from a single source is not favoured here, but it cannot yet be dismissed.

The nomenclature of this genus will ultimately have to be established by further testing of the hypotheses presented here, and perhaps by reference to conclusions reached in respect of other taxa with similar wide distributions and generally uniform characteristics. Amongst the latter are the living brown and black bears, as well as a wide variety of other carnivores, notably canids and felids.

SUMMARY

Available material of *Agriotherium africanum* from the latest Miocene/early Pliocene Varswater Formation at Langebaanweg is described. This species was found to be as variable as other bears of comparable size, this being in part due to marked sexual dimorphism.

The depositional environment and likely habitat and habits of the Langebaanweg *Agriotherium* are discussed. It is suggested that it was a large woodland carnivore, remains of which were transported to their points of discovery by a river which then met the sea in the vicinity of Langebaanweg. The transporting agent, and hyaenas, rodents, and fires contributed to the post-mortem damage exhibited by specimens.

Agriotherium was evidently descended from late Miocene *Indarctos*, the more significant evidence in support of this hypothesis being as follows:

1. There was an increase of size with time in the *Indarctos*-*Agriotherium* lineage, and advanced *Indarctos* may be little or no different in size to *Agriotherium*.
2. The skull characters of advanced *Indarctos* (e.g. *I. atticus* from Samos; *Indarctos* from Florida) are shared by *Agriotherium* (e.g. the Langebaanweg specimen L45062). Observable differences reflect further development of trends already evident in the *Indarctos* lineage. Significant shared characteristics are a relatively short and broad snout, with the posterior palatine incisure in line with the M² metacones, large zygomatics and sagittal crest, and similar basi-cranial region, including absence of the alisphenoid canal.

3. There is little or no difference in the dentitions of advanced *Indarctos* and *Agriotherium*. For example, the incisors, canines, P₄'s, M₁'s, M₂'s and M₃'s may be morphologically indistinguishable. Differences that do exist reflect trends already evident in the *Indarctos* lineage. For example:

- (i) There was a progressive reduction in the size and number of anterior premolars in the *Indarctos*-*Agriotherium* lineage, with their principal cusps becoming progressively lower crowned and indistinct. However, *Agriotherium* sometimes has *Indarctos*-like upper premolars (e.g. *A. insigne*, NMB-MP549), while *Indarctos* may have *Agriotherium*-like lower anterior premolars (e.g. *I. atticus*, NMW-Samos 1912, 29).
- (ii) The shearing elements of the carnassials in the *Indarctos*-*Agriotherium* lineage are progressively developed, as are the buccal cusps of M₁ and M₂, which also have a shearing function. There is a corresponding reduction in the crushing elements of the posterior cheek teeth. For example, while the M₂ of *Indarctos* is distinguished from that of *Agriotherium* by the presence of a talon, this feature is progressively reduced in time. In advanced *Indarctos* it may be small (e.g. *I. punjabiensis*, GSI-D12), while vestiges of a talon may be present in *Agriotherium* (e.g. the Langebaanweg specimen L47698).
- (iii) As a general rule the P₄ of *Agriotherium* is distinguished from that of *Indarctos* by the presence of a parastyle, but this cusp may be present in advanced *Indarctos* (e.g. Samos *I. atticus*; most North American specimens).

4. A double-cusped P₄ protocone lobe is characteristic of European *Indarctos*, and is also found in some European and African *Agriotherium* specimens (e.g. *A. insigne*, NMB-MP549; Langebaanweg L2045 and others), although the P₄ antero-internal cusp is sometimes absent (e.g. *A. insigne*, Gervais (1859) specimen; Langebaanweg, L41404). The fact that this cusp is sometimes absent in *A. insigne*, and that in those specimens postdating L2045 it is reduced or absent, indicates that there was a tendency in European-African *Agriotherium* to lose the antero-internal cusp. A similar tendency is evident in advanced Asian and North American *Indarctos* (e.g. *I. punjabiensis*, GSI-D6; Florida *Indarctos*), while the antero-internal cusp is always absent in the *Agriotherium* from these continents. This common tendency in *Indarctos* and *Agriotherium* indicates a close relationship, while the examples cited suggest that the European/African and Asian/North American *Indarctos*-*Agriotherium* lineages evolved independently and at different rates later in their history.

The primary *Indarctos*-*Agriotherium* lineage was European and comprised *I. vireti*, *I. arctoides*, *I. atticus* and *A. insigne*, with *I. anthracitis* as an aberrant, probably island-dwelling offshoot. *Indarctos* emigrated to Africa, probably late in the Miocene, and an *Agriotherium* (*A. africanum*) very similar to the European *A. insigne* was evolved on this continent. Advanced *Indarctos* also migrated eastwards and the Asian/North American lineage is comprised of species of

Indarctos and *Agriotherium* postdating *I. atticus*. Pending further studies, most existing species names of these genera are retained.

It is suggested that either all *Indarctos*, or all later *Indarctos* (*I. atticus* and younger species) should be referred instead to *Agriotherium*, although the *status quo* is maintained for the present.

A modified suprageneric classification of later Ursidae is proposed. The species of *Ursavus* are included in a new subfamily, the Ursavinae. The Agriotheriinae are divided into two tribes, namely, Agriotheriini (*Indarctos*-*Agriotherium*) and the Ailuropodini ('*Ursavus*' *depereti*-*Ailuropoda melanoleuca*). The Ursinae and Tremarctinae are reduced to the status of tribes within a reconstituted subfamily Ursinae.

ACKNOWLEDGEMENTS

I am greatly indebted to the many persons who assisted directly and indirectly in the study of the Langebaanweg *Agriotherium*. They include Drs G. de Beaumont (Geneva), B. Engesser (Basel), A. W. Gentry (London), L. Ginsburg (Paris), J. Jewell (London), C. A. Repenning (Menlo Park, California) and E. Thenius (Vienna) who provided access to, and/or casts of, specimens in their care. Drs A. J. Tankard (Knoxville, Tennessee) and R. H. Tedford (New York) provided information on geological and palaeontological matters respectively. Almost all the photographs of specimens were made by Miss J. Nolte, while Mr A. Byron printed Figures 27 and 32. Miss L. Scott prepared Figure 34, Mrs P. Eedes typed the manuscript, and the South African Air Force provided the aerial photograph for Figure 26. Drs R. G. Klein (Chicago) and B. Kurtén (Helsinki) reviewed early drafts of the manuscript.

The Langebaanweg Research Project is supported by Chemfos Ltd, the South African Council for Scientific and Industrial Research, and the Wenner-Gren Foundation for Anthropological Research (Grant no. 2752-1834), and the assistance of these organizations is gratefully acknowledged.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula longilliriti Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

Q. B. HENDEY

AGRIOTHERIUM (MAMMALIA, URSIDAE)
FROM LANGEBAANWEG, SOUTH AFRICA, AND
RELATIONSHIPS OF THE GENUS

507,68

VOLUME 81 PART 2

FEBRUARY 1980

ISSN 0303-2515

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Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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- 'Smith (1969) describes ...'
- 'Smith (1969: 36, fig. 16) describes ...'
- 'As described (Smith 1969a, 1969b; Jones 1971)'
- 'As described (Haughton & Broom 1927) ...'
- 'As described (Haughton *et al.* 1927) ...'

Note: no comma separating name and year
pagination indicated by colon, not p.
names of joint authors connected by ampersand
'*et al.*' in text for more than two joint authors, but names of all authors given in list of references.

(b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc. to the year for more than one paper by the same author in that year, e.g. Smith (1969*a*, 1969*b*) and not Smith (1969, 1969*a*).

For books give title in italics, edition, volume number, place of publication, publisher.

For journal article give title of article, title of journal in italics (abbreviated according to the *World list of scientific periodicals*, 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, pagination (first and last pages of article).

Examples (note capitalization and punctuation)

- BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
- FISCHER, P.-H. 1948. Données sur la résistance et de la vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.
- FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Etudes sur les échanges respiratoires des littorines. *Archs Zool. exp. appl.* 74: 627.
- KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.
- KOHN, A. J. 1960*b*. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.
- THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume **81** Band
February **1980** Februarie
Part **2** Deel



ON THE VALIDITY OF THE THEROCEPHALIAN
FAMILY LYCOSUCHIDAE
(REPTILIA, THERAPSIDA)

By

J. A. VAN DEN HEEVER

Cape Town . Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town 8000

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na gelang van die
beskikbaarheid van stof

Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad 8000

OUT OF PRINT/UIT DRUK

1, 2(1-3, 5-8), 3(1-2, 4-5, 8, t.-p.i.), 5(1-3, 5, 7-9),
6(1, t.-p.i.), 7(1-4), 8, 9(1-2, 7), 10(1-3),
11(1-2, 5, 7, t.-p.i.), 15(4-5), 24(2), 27, 31(1-3), 32(5), 33

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Kopieregnavrae aan die Suid-Afrikaanse Museum

ISBN 0 908407 85 8

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

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By

J. A. VAN DEN HEEVER

South African Museum, Cape Town

(With 9 figures)

[MS. accepted 29 November 1979]

ABSTRACT

The taxonomic position of the therocephalian family Lycosuchidae is discussed in the light of published accounts and a re-examination of most of the type material, together with additional information from undescribed specimens of early therocephalians. It is shown that the primary distinguishing characteristic of the Lycosuchidae which separates it from the Pristerognathidae, i.e. two simultaneously functional canines in each maxilla, is based on a misinterpretation. It is therefore concluded that the family consists of an unnatural grouping of members of the Pristerognathidae and should consequently be regarded as invalid.

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INTRODUCTION

The early Therocephalia of the upper Permian Tapinocephalus Zone (Dinocephalian and Pristerognathus/Diictodon Assemblage Zones of Keyser & Smith 1979) of the Beaufort Series of the South African Karoo are generally poorly understood in comparison with other therapsid groups such as the Dicynodontia and the Cynodontia, mainly as a result of the intractable matrix in which the material is usually found. Since the dentition of an unprepared specimen is often its most distinctive feature the number and position of the teeth have been predominantly used in the past to distinguish between the various taxa of the group. Consequently, serious doubts have only recently been raised about the naturalness of taxa which have existed in the literature, e.g. the Lycosuchidae (Haughton & Brink 1955). Since the family Lycosuchidae was established its relatively rare members, identified principally by the possession of two maxillary canines, have always been regarded as closely allied to

the more abundant family Pristerognathidae, contemporary therocephalians with one maxillary canine. Most authors (Haughton & Brink 1955; Kermack 1956; Romer 1956; Watson & Romer 1956; Boonstra 1969) who have discussed the early Therocephalia have placed great taxonomic weight on the number of canines and consequently the concept of double-canined therocephalians is widespread in the literature. Illustrations of early therocephalians usually present the double-canined *Lycosuchus* as a general representative of the group (Du Toit 1954; Romer 1956, 1966).

Kermack (1956) demonstrated in the Therocephalia and the Gorgonopsia the existence of two upper canine positions which alternate in housing a single functional canine. According to Hopson (1964) this is also the case in the cynodont *Thrinaxodon liorhinus* and probably most other cynodonts as well. From this it is to be expected that while the functional canine was being replaced, the animal would have two canines of different ages in each maxilla, superficially similar to the condition frequently observed in living mammals when the permanent canine is in the process of replacing the milk canine (Fig. 1). Kermack also described a lycosuchid *Trochosaurus major* with two erupted canines and states that the possession of two simultaneously functional canines was primitive for Therocephalia. This idea probably stems from the view that a similar condition was thought to typify spenacodont pelycosaurs, the presumed ancestors of therapsids.

In an important paper Mendrez (1972) established the existence of an incipient *crista choanalis* in the pristerognathids *Pristerognathus polyodon* and *Ptomalestes avidus*, situated on the inner surface of the maxilla medial to the canines. She interpreted this structure as the first step on the way to the development of a bony secondary palate as in mammals. Since the gorgonopsian maxilla is completely smooth in this area (Kemp 1969), this structure makes it possible to distinguish readily between the otherwise very similar snout fragments or isolated maxillae of therocephalians and gorgonopsians. Mendrez



Fig. 1. Stereophotograph of the left maxilla of *Felis caracal* (SAM-ZM38191) to show the eruption of the permanent canine anterolingual to the milk canine. Scale = 10 mm.

(1972) also noted the presence of two canine positions in *Pristerognathids* (but did not cite Kermack's prior discovery of this fact) and states at page 2961: '*Pristerognatus polyodon* ainsi que *Ptomalestes avidus* possèdent également une autre caractéristique qui, selon les descriptions classiques, était, parmi les *Pristerosauria* de la zone à *Tapinocephalus*, la propriété exclusive des *Lycosuchidae*, à savoir la présence de deux canines de chaque côté de la tête. Ceci diminue le nombre déjà faible des caractères opposant ces deux familles. Il est fort probable que le *Pristerognathidae* décrits comme présentant un diastème entre la canine et les postcanines possédaient à cette place une seconde canine.' From this she concluded that the *Pristerognathidae* and the *Lycosuchidae* probably form a single family. However, from her statement it appears as if the *Pristerognathidae* possessed, like the *Lycosuchidae*, two functional canines in each maxilla and thus that the accepted definition of the *Lycosuchidae* should include the *Pristerognathidae* as well.

In summary, the only distinguishing characteristic of the family *Lycosuchidae* that at present still appears to separate it from the *Pristerognathidae* is the presence of two functional canines in each maxilla. In an effort to determine the validity of this morphological distinction, and thus of the family *Lycosuchidae*, a detailed study of the mode of replacement of the upper canines was undertaken. This study is intended to resolve the question of whether the two canines were fully mature and remained simultaneously functional for a long period of time (as assumed by most authors), or whether the condition represents a short-lived phenomenon in the replacement process, representing a stage during which the new canine is well erupted but the old functional canine has not yet been shed. The latter interpretation implies that the double-canined condition is a short segment of the normal replacing cycle of all early thercephalians and that there is no valid basis for taxonomically separating the double-canined forms (*Lycosuchidae*) from the *Pristerognathidae*.

HISTORICAL REVIEW

The first early thercephalian possessing two maxillary canines was described by Broom (1903a) as *Lycosuchus vanderrieti* (Figs 2-3). According to Broom the only other theriodont known at that time which possessed two canines in each maxilla was the Albany Museum specimen of the cynodont ? *Cynognathus leptorhinus* Seeley (currently placed in *Cynognathus crateronotus*). However, in an addendum to the description of *Lycosuchus vanderrieti*, Broom (1903a) notes that ? *Cynognathus leptorhinus* is similar to *Cynognathus platyceps* and that the other known species of *Cynognathus* all had only one canine; therefore, the double-canined condition in this specimen was regarded by him as temporary. Broom also drew attention to the type of *Trirachodon kannemeyeri* Seeley which on one side of the snout, in front of the canine, shows the tip of a second canine similar to that in both *Cynognathus* and *Lycosuchus*. Broom (1903a) felt that the anterior canine in all these genera is the morphological equivalent of the permanent mammalian canine and the

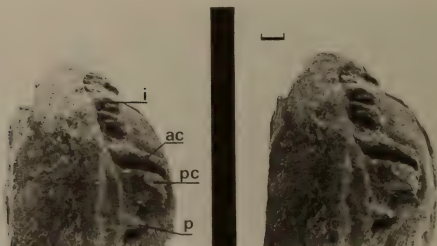


Fig. 2. Stereophotograph of the right maxilla of the type skull of *Lycosuchus vanderrieti* (Stellenbosch D173) to show the canines. The specimen is covered with polymethylmethacrylate for preparation in acid. Scale = 10 mm.

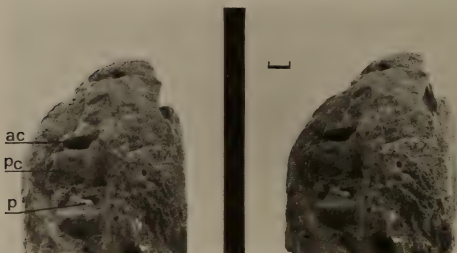


Fig. 3. Stereophotograph of the left maxilla of the type skull of *Lycosuchus vanderrieti* to show the canines. The specimen is covered with polymethylmethacrylate for preparation in acid. Scale = 10mm.

posterior canine is the equivalent of the deciduous canine of mammals. He also stated that both teeth may, however, have been functional for some time in *Lycosuchus* and the higher theriodonts because the posterior canine which developed first is more powerful and the anterior canine is 'peculiarly specialized' as if developed for a different function. The suggestion of separate functions was due to his observation that both the anterior and the posterior borders of the anterior tooth are serrated, whereas only the posterior border of the posterior tooth appeared to be serrated.

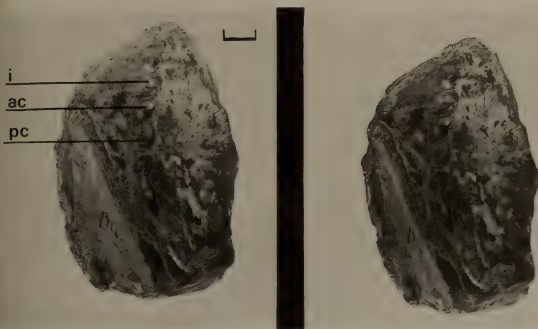


Fig. 4. Stereo photograph of the left maxilla of the type specimen *Trochosuchus acutus* (SAM-1076) to show the canines. Scale = 10mm.

Broom (1903b) described the isolated maxilla of a second therocephalian possessing two canines as *Lycosuchus mackayi*. Not until five years later (Broom 1908), however, when describing the double-canined *Hyaenasuchus whaitsi*, does he mention the fact that he now regards both canines in these early therocephalians as being *simultaneously* functional with neither of them being a replacement tooth. In the same article Broom described the anterior part of a small therocephalian skull as *Trochosuchus acutus*, noting the presence of two maxillary canines, the anterior being the smaller (Fig. 4).

Broom (1915) described *Trochosuchus major* specifically, stating that neither of the two canines in the maxilla is a replacement tooth and that in the light of the descriptions of *Lycosuchus*, *Hyaenasuchus* and *Trochosuchus* he regards these genera as having two large canines functioning simultaneously in each maxilla.

Haughton (1915) in his description of *Trochosaurus intermedius* followed Broom in interpreting the two canines present in each maxilla as being simultaneously functional, notwithstanding the fact that they differed in size and that a replacement tooth was situated medial to the anterior canine in each maxilla.

In his book on the mammal-like reptiles of South Africa, Broom (1932) redescribed all of the species with two canines in each maxilla and stated that both teeth are simultaneously functional because more than a dozen specimens were then known to possess this arrangement of teeth. He regarded them as a

group separate from the Pristerognathidae but did not formally establish a new family for them. (*Lycosaurus mackayi* at his p. 50 is an error and should read *Lycosuchus mackayi*.) He also synonymized *Trochosaurus intermedius* (Haughton, 1915) with *Trochosuchus major* (Broom, 1915) under the name *Trochosaurus major*. He retained the genus *Trochosuchus* for the single specimen of *Trochosuchus acutus* (Broom, 1908).

A third specimen of *Trochosaurus major* was described by Boonstra (1934) who indicated in the text as well as in the figures that the canines were undergoing replacement. He also noted the relatively broad epipterygoid which is narrowest in the middle and expanded dorsally and ventrally.

Broom (1936a) described *Trochorhinus vanhoepeni* as closely allied to *Trochosaurus major* and possessing two canines of unequal size, the larger being anterior.

Broom (1936b) described *Trochosaurus dirus* as having two large functional canines in each maxilla. However, the canines are at different stages of development and the roots of their eventual replacements are visible medially. He notes that both canines are functional and situated so close together that they probably functioned as one tooth. Furthermore he states that: '... each anterior canine has a very young replacing tooth; but the posterior canine on the left is being replaced by an already well-developed successor. On the right side the specimen is imperfect but the inner canine is of large size and apparently functional. Probably the outer canine is shed or being absorbed.'

No new early therocephalian specimens showing double upper canines were described after 1936. Romer (1945) included all of the above-mentioned genera in the Pristerognathidae.

Although Broom (1932) developed the rather loose concept of double-canined therocephalians, it was actually Houghton & Brink (1955) who established the family Lycosuchidae, for which they gave the following diagnosis: 'Medium-sized therocephalians with two large functional canines in each maxilla.' They listed the species as: *Hyaenasuchus whaitsi* Broom, 1908; *Lycosuchus vanderrieti* Broom, 1903 (not 1902 as given by Haughton & Brink); *Lycosuchus mackayi* Broom, 1903; *Trochorhinus vanhoepeni* Broom, 1936; *Trochosaurus major* (Broom, 1915), and *Trochosaurus dirus* Broom, 1936. The single specimen of *Trochosuchus acutus* was referred by them to the family Akidnognathidae. Tatarinov (1974) ascribes the establishment of the family Lycosuchidae to Haughton (1924). The references in Tatarinov's article reveal that the paper in question was actually published in 1925; however, in this paper Haughton retained the double-canined forms in the family Pristerognathidae.

Shortly thereafter, Watson & Romer (1956) followed Romer (1956) who independently established the family Trochosuchidae comprising the same genera as those placed by Haughton & Brink (1955) in the Lycosuchidae. They also synonymized *Trochosaurus* Haughton, 1915, with *Trochosuchus* Broom, 1908. Watson & Romer (1956) diagnosed the family Trochosuchidae as: 'Large

therocephalians which resemble the Pristerognathidae in fundamental features of their structure but differ in having a much lower skull with a broad and rather flattened snout, a sagittal crest never elevated and the occiput transversely widened. They may have six incisors and normally two canines, each separately replaced.' Since their classification is predated by that of Haughton & Brink (1955) the name Lycosuchidae has precedence and has been used by nearly all subsequent authors, e.g. Boonstra (1969, 1971, 1972), Mendrez (1972), and Tatarinov (1974); Lehman (1961: 232), however, incorrectly follows Watson & Romer (1956). Von Huene (1956) retains the members of the Lycosuchidae within the Pristerognathidae.

In spite of having synonymized *Trochosaurus* with *Trochosuchus* (Watson & Romer 1956), Romer (1966), synonymized the Lycosuchidae of Haughton & Brink (1955) with a new family, the Trochosauridae. This was apparently done to facilitate the inclusion of *Trochosuchus* in another family, the Alopecodontidae (Romer 1966). However, Haughton & Brink (1955) had placed *Trochosuchus* in the Akidognathidae (defined as having one small canine in front of the large functional canine) a family not recognized by Romer (1966), and they described the Alopecodontidae as therocephalians with two small canines in front of the large functional canine in the maxilla. The weathered type specimen of *Trochosuchus acutus* (SAM-1076) in the South African Museum has one canine in the right maxilla and two canines in the left maxilla, the anterior being the smaller (Fig. 4). However, the last incisor appears to lie within the maxilla when viewed laterally and may have been mistaken for a small canine by Romer.

The genera included by Watson & Romer (1956) in the Trochosuchidae (Lycosuchidae) do not have larger skulls than those early therocephalians possessing a single maxillary canine, and an examination of the available material indicates that the other diagnostic differences of the family can be attributed to post-mortem distortion. Consequently, in a later description of the Lycosuchidae, Boonstra (1969) characterizes the family as: 'Early fairly large Therocephalia with fairly broad flattened skulls with two functional canines in the maxilla, advanced broadened epipterygoid and low sagittal crest. Otherwise very similar to pristerognathids. With four monotypic genera.' However, as Mendrez (1972) quite rightly points out, the so-called broad epipterygoid of the Lycosuchidae is actually known in one specimen only, *Trochosaurus major* (BMNH R5747), and it is, in fact, no broader than that of the pristerognathid *Ptomalestes avidus*.

MATERIAL AND TECHNIQUES

The type material of *Tapinocephalus* Zone therocephalians at the South African Museum was examined. In addition a complete therocephalian skull (G.S. C60) with lower jaw, lacking only the occipital bones, was borrowed from the Geological Survey. The medial aspect of the right maxilla of this specimen was carefully prepared by mechanical means to show the canines.

The type skull of *Lycosuchus vanderrieti* (D173), on loan from the University of Stellenbosch, is currently being prepared in an 11 per cent solution of formic acid owing to the extreme hardness of the matrix. It is at present still covered with polymethylmethacrylate (Figs 2–3), but the double canines are well preserved and have been examined.

Other material was prepared mechanically where necessary. In addition, the right maxilla of an unidentified species of therocephalian, SAM-K317 (identified as therocephalian according to the method of Mendrez (1972)), was sectioned frontally on a Beuhler Isomet Low Speed Saw at intervals of 2 mm. One section was stained with Alizarin Red S in a 4 per cent solution of potassium hydroxide to show the resorption of the canine root.

All photographs were taken on Kodak Panatomic-X film with a stereo apparatus built by N. J. Eden of the South African Museum.

DESCRIPTION AND DISCUSSION

The inner surface of the left maxilla of therocephalian SAM-K317 shows a distinct canine boss which contains the two canine alveoli (Fig. 5). The relative positions of the roots are visible as two smaller bulges separated by a shallow vertical sulcus. This condition can also be seen in the type of the pristerognathid *Ptomalestes avidus*, SAM-11942. The functional canine lies in the anterior alveolus and is broken off at the alveolar border. No tooth is externally visible in the posterior alveolus. The right maxilla of SAM-K317 shows the same features as does the left side, but a frontal section through the posterior alveolus shows the root of an old canine being resorbed from the alveolar border upwards (Figs 5–6).

The skull of Geological Survey specimen C60 has been compressed laterally, but in lingual view the maxilla clearly shows the canine boss with the functional canine in the anterior alveolus (Fig. 7). A replacement canine of which the tip is serrated both anteriorly and posteriorly is erupting from the posterior alveolus. This condition is identical to that in the left maxilla of *Lycosuchus*

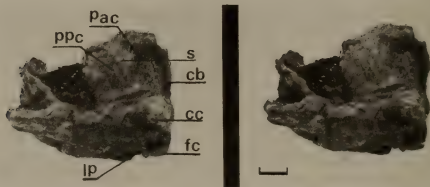


Fig. 5. Stereophotograph of the medial surface of the left maxilla of an unidentified pristerognathid (SAM-K317) showing the boss containing the canine alveoli. Anterior is to the right. Scale = 10 mm.

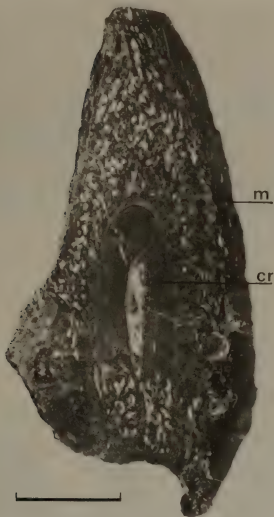


Fig. 6. Frontal section through the posterior canine alveolus of the right maxilla of an unidentified pristerognathid (SAM-K317) to show the resorption of the old canine root and its replacement by spongy bone.

Scale = 10 mm.

vanderrieti except that in the latter the younger tooth lies in the anterior position (Fig. 3).

See externally only, G.S. C60 would have to be classified as a lycosuchid according to the accepted definition of the family. However, the diameter of the posterior alveolus is the same as that of the anterior and much larger than that of the erupting canine. This suggests that the posterior alveolus was probably occupied previously by a large canine and that the immature tooth is not the first to have erupted in that position. Medial to the functional canine (Figs 7-8) an unerupted replacement canine is visible where the bone of the

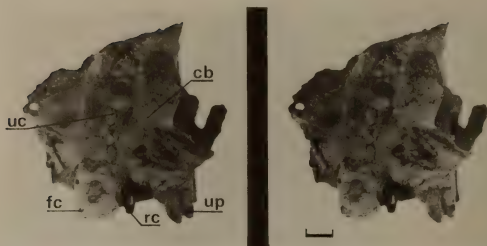


Fig. 7. Stereophotographs of the medial surface of the right maxilla of an unidentified pristerognathid (G.S. C60) showing the boss containing the canine alveoli and the sequence of canine replacement. Scale = 10 mm.



Fig. 8. Stereophotographs of a ventral view of the right maxilla of an unidentified pristerognathid (G.S. C60) to show the sequence of canine replacement. Scale = 10 mm.

medial wall is damaged. In this 'lycosuchid', then, there is direct evidence that the sequence of canine eruption alternates between the two alveoli in such a way that the time lapse between the eruption of teeth in the two alveoli produces a single functional canine at a time. This is also the most likely interpretation of the condition in the type of *Lycosuchus vanderrieti*. Specimens with two large canines in the same maxilla represent the terminal stages of the older tooth of the pair.

Since the second canine is older than the first in *Lycosuchus vanderrieti*, it would naturally be more powerful than the immature tooth, and since both tips of the posterior canines in *Lycosuchus* are damaged, Broom (1932) had no grounds for stating that the anterior canines are 'peculiarly specialized' for a different function. In fact, specimens of therocephalians which have complete canines show serrations at the tips of these teeth both in front and behind, regardless of whether the tooth is in the anterior or posterior position.

Kermack (1956) regards the single lycosuchid specimen (*Trochosaurus major*, BMNH R5747) described in his paper as one of the most primitive of the therocephalians because it has two functional canines in each maxilla (Fig. 9). By his own description (Kermack 1956: 114) the roots of replacement canines can be seen in a fracture lying lingual to each of the canines in the right maxilla. The anterior of this pair is in a more advanced stage of development than the posterior, which strongly suggests that the two large functional teeth are also of different ages. On the left, the fracture is such that the replacement teeth cannot be seen but the large canines are clearly also of differing ages since the anterior canine was still in the process of erupting and has a wide-open pulp cavity. This indicates not that both teeth were functional at the same time but rather that replacement was taking place at the time of death. However, Kermack (1956: 115) states: 'This specimen compares closely with the two specimens of *Aelurosaurus* (R339 and R855a). The only essential difference is that, in the two gorgonopsids the pair of alveoli in the maxilla each alternately bears the functional canine, while in the therocephalian each bears a functional tooth simultaneously. The difference is one of timing only.'

Kermack (1956: 121) notes further that in sphenacodont pelycosaur such as *Dimetrodon*, as well as in *Trochosaurus*, two functional canines were present in each maxilla and elsewhere (Kermack 1956: 130) he states: 'As in *Dimetrodon* there was a pair of functional upper canines on each side in these primitive therocephalia, and they were replaced alternately. The functional replacement for each of the pair was the next number of its own tooth family. Like *Dimetrodon* when one of the upper canines was being replaced, these Therocephalia must have had but one functional canine on that side of the jaw.'

Kermack (1956) apparently implies here that in *Dimetrodon* and *Trochosaurus*-like primitive therocephalians the double canine condition was the prevailing one, whilst the period during which only one canine was functional was, in fact, of a comparatively short duration, i.e. there were normally two upper canines functioning simultaneously.

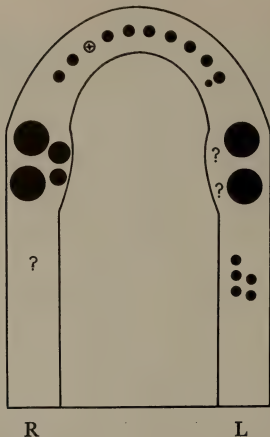


Fig. 9. Diagram from Kermack (1956) to show the canines and canine replacements of *Trochosaurus major* (BMNH R5747).

R = right, L = left.

The South African Museum holds at least 112 specimens of early theropcephalian skulls and skull fragments in which the canines can be seen. Of these, fourteen specimens possess two canines in either one or both of the maxillae, including the above-mentioned types. This ratio of roughly one specimen with double canines for every seven with a single canine per maxilla illustrates the relative scarcity of the two-canine condition and indicates that the period during which two canines were externally visible was probably of relatively short duration. In no South African Museum specimen with double canines are there any indications that the teeth are of the same age and, from the literature cited above, it is also clear that in *all* described specimens of Lycosuchidae the canines are also staggered in age. It is highly improbable that in carnivores such as the Therocephalia, in which the tips of the canines are serrated both anteriorly and posteriorly, these teeth would have functioned optimally as a closely packed unit. Not only would the efficiency of penetration be impaired

by the bulky 'unit' composed of two large teeth, but also, since some of the serrations would be obscured, the teeth would tear less efficiently as well. Therefore, it seems more likely that these animals possessed a single piercing canine of long functional duration and that the period of replacement, during which two canines were externally visible in each maxilla, was as short as possible. This is indicated by the relatively few specimens actually showing this condition. The *functional* replacement for each canine would then not be the next tooth of its own family (i.e. in the same tooth position), but the next tooth erupting from the other canine alveolus. This model of canine tooth replacement is supported by the work of Edmund (1960) who, contrary to the observation of Kermack (1956), found that in *Dimetrodon* the pair of canines in each maxilla were only occasionally functional at the same time and usually alternated so that only one tooth was functional at a time.

CONCLUSIONS

Kermack (1956) is correct in stating that in the Therocephalia the two canine alveoli each bore the functional canine alternately, but he is incorrect in assuming that in the Lycosuchidae, e.g. *Trochosaurus*, both alveoli normally bore functional canines simultaneously. In view of the importance of canines in carnivore dentitions it is to be expected that the replacement of any fang will develop at such a time and replace the mature canine in such a way that the animal is never without at least one functional canine in each maxilla. This necessitates a period of time when the erupting replacement coexists with the old functional tooth. Because of the distinct advantages of the single over the double functional canine condition, the actual period of time in which the two canines were externally visible was probably kept as short as possible.

The Lycosuchidae is therefore not a separate primitive therocephalian family but consists of members of the Pristerognathidae in which death occurred while the erupting replacing canine was visible externally. *Lycosuchus vanderreti* (Figs 2-3) is an especially good example of this condition. Therefore the family Lycosuchidae (=Trochosauridae) represents an unnatural grouping of members of the Pristerognathidae, and it is suggested here that it be invalidated.

ACKNOWLEDGEMENTS

I wish to thank the following persons: Mrs K. Rial and Mr N. J. Eden, both of the Department of Palaeontology at the South African Museum for, respectively, preparation and photography, Professor W. J. Verwoerd of the Department of Geology at the University of Stellenbosch, and Dr A. W. Keyser of the Geological Survey in Pretoria for the loan of specimens, Dr J. A. Hopson of the University of Chicago for critically reading the manuscript, and Mrs P. Eedes and Mrs G. E. Blaeske, of the South African Museum, for typing.

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ABBREVIATIONS

a.c.	anterior canine
c.b.	canine boss
c.c.	crista choanalis
c.r.	canine root
f.c.	functional canine
i.	incisor
l.p.	lower postcanine
m.	maxilla
m.c.	milk canine
o.a.	old alveolus
p.	postcanine
p.a.c.	position of anterior canine
p.c.	posterior canine
p.ca.	permanent canine
p.p.c.	position of posterior canine
r.c.	replacing canine
s.	sulcus
u.c.	unerupted canine
u.c. tip	tip of unerupted canine
u.p.	upper postcanines
BMNH	British Museum of Natural History
G.S.	Geological Survey, Pretoria
SAM	South African Museum.

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

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Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (*Lembulus*) *bicuspidata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspidata* Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierti Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- (c) Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

J. A. VAN DEN HEEVER

ON THE VALIDITY OF THE
THEROCEPHALIAN FAMILY LYCOSUCHIDAE
(REPTILIA, THERAPSIDA)

ANNALS

OF THE SOUTH AFRICAN MUSEUM

CAPE TOWN



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- BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
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(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume 81 Band
February 1980 Februarie
Part 3 Deel



DEVONIAN FISH AND PLANTS
FROM THE BOKKEVELD SERIES
OF SOUTH AFRICA

By

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The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
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Obtainable from the South African Museum, P.O. Box 61, Cape Town 8000

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na gelang van die
beskikbaarheid van stof

Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad 8000

OUT OF PRINT/UIT DRUK

1, 2(1-3, 5-8), 3(1-2, 4-5, 8, t.-p.i.), 5(1-3, 5, 7-9),
6(1, t.-p.i.), 7(1-4), 8, 9(1-2, 7), 10(1-3),
11(1-2, 5, 7, t.-p.i.), 15(4-5), 24(2), 27, 31(1-3), 32(5), 33

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Kopieregnavrae aan die Suid-Afrikaanse Museum

ISBN 0 908407 88 2

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

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(With 14 figures and 1 addendum)

[MS. accepted 20 September 1979]

ABSTRACT

Fossil fish and plants from upper strata of the Bokkeveld Series of Barrydale, Cape Province, Republic of South Africa, are described. The fishes are represented by arthrodire placoderms, *Barrydalaspis theroni* gen. et sp. nov., a phlyctaenaspid arthrodire and, possibly, *Groenlandaspis*; an acanthodian spine indistinguishable from *Gyracanthides warreni* White; and an egg case. The plants are represented by lycopods: *Archaeosigillaria plumsteadiae* sp. nov., *A. cf. picosensis* Kräusel & Dolianiti, and two different types of lycopod endocortical cast. The fishes and plants are compared with those in Australia, Antarctica, North America and South America, and it is concluded that these Bokkeveld fossils are either Middle or Upper Devonian.

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INTRODUCTION

In 1974 a small collection of fossil fish and plants was sent to one of the authors (B. G.) for identification by Dr J. N. Theron of the Geological Survey of South Africa. The material comes from the upper strata of the Bokkeveld Beds at Barrydale, Cape Province, Republic of South Africa. Precise locality information is not available.

The Bokkeveld Series is reputed to be of Devonian age (Du Toit 1939) and therefore the presence of fish is of significance because, with one possible exception, fish have not previously been recorded from the Devonian of South Africa. This one possible exception is a reference to the occurrence of *Machae-racanthus* in the Bokkeveld Beds which is given without detail by Du Toit (1939: 222). It is possible that Du Toit extracted this record from Schwarz (1900) who referred to a fossil fish spine. At the very best, therefore, Devonian fish from southern Africa are very poorly known and this collection adds a new dimension to our rapidly increasing knowledge of Devonian fish from the Southern hemisphere.

The primary purpose of this paper is to describe these fishes. The fish are associated with a few plant remains and these are described and discussed (W. G. C. & A. J. H.). A few notes are added concerning the age of the Bokkeveld Beds based on comparisons of the fish and plants with those preserved in presumed contemporaneous strata in North and South America, Antarctica, Australia and west Africa.

The fish are represented mainly by placoderms, but an acanthodian and the impression of a large egg case are also present. This last is particularly interesting since the form of the egg case is similar to those attributed to chimae-roids which are not known prior to the Jurassic. The plants are represented by several types of lycopods. All the fossils are poorly preserved, the majority being represented as impression or internal casts. The matrix is a texturally variable and poorly bedded micaceous siltstone. Because of this and the type and condition of the contained fossils, it appears as if the sediment was deposited in a freshwater environment and that the fossils lived in the place of sedimentation.

The specimens referred to in this paper come from the collections of the South African Museum, Cape Town and from the Geological Survey, Cape Office. The former are prefixed by SAM; the latter are left unprefix, simply being quoted by the field number.

THE FISH REMAINS

ARTHRODIRES

A number of facts have made the study of the arthrodires difficult; only impressions of the plates remain; with few exceptions the plates are isolated and sometimes broken, making it difficult to associate parts of animals; there

is some degree of post-mortem deformation with resulting distortion. Nevertheless, the margins of the plates are perfectly angular, ruling out the possibility of post-mortem/pre-depositional transportation. Among the specimens several show associated ventral thoracic armour and on the basis of these two types of arthrodire can be recognized. Some isolated plates of the lateral aspect of the trunk shield can be referred to one or other of these types. It has been decided to name one of these because it is distinctive from other named arthrodires. The second arthrodire type shows a general similarity to named arthrodires from elsewhere. To avoid cluttering the already burdensome literature with yet another name, this is referred to as a 'phlyctaenaspid arthrodire' with the implication that what little is known of this form is similar to *Neophlyctaenius* and presumed close relatives. Additionally, specimens of a head and a piece of a large arthrodire are briefly mentioned.

Order ARTHRODIRA

Suborder PHLYCTAENIOIDEI Miles 1973

Infraorder and Family incertae sedis

Genus *Barrydalaspis* gen. nov.

(Figs 1-4, 6A)

Etymology

From Barrydale, South Africa, the area in which these fossils are found.

Diagnosis

Phlyctaenioid with short, broad ventral thoracic armour; spinal long with denticles along the medial edge, spinals set at a very divergent angle; subpectoral emargination broad; interolateral with prominent transverse groove; anterior ventrolateral of either side meeting its partner in the mid-line; anterior dorsolateral with a prominent groove on the lateral face of the anteroventral corner; ornament consisting of small, simple tubercles; body behind thoracic shield at least partially covered with scales.

Type species

Barrydalaspis theroni sp. nov.

Barrydalaspis theroni sp. nov.

Etymology

Named after Dr J. N. Theron who brought this material to the attention of the authors.

Holotype

SAM-K4647, the impression of the ventral thoracic armour from the Bokkeveld Series of Barrydale, Cape Province, South Africa.

Other material

SAM-K4648-50, K4770-73, K4766, K4779, K4785, K4789, K4791, and an anterior dorsolateral plate preserved on K4798.

Diagnosis

As for genus, only species.

Remarks

The ventral thoracic armour shows a superficial resemblance to that of the petalichthyid *Lunaspis* (see Gross 1961); the armour is short and broad and the spinals are set at a divergent angle. However, unlike *Lunaspis*, *Barrydalaspis* shows well-differentiated posterior ventrolaterals. (Gross (1961) describes two pairs of plates lying behind the anterior ventrolaterals in *Lunaspis*, the posterior ventrolaterals and the postero-ventrals. These are interpreted as body scales by Miles & Young (1977) and their interpretation is accepted here.) Furthermore, the dorsal part of the armour is similar to that of a phlyctaenoid and unlike that of a petalichthyid in showing a 'ball and socket' dermal neck joint and a large posterior dorsolateral.

The anterior ventrolateral (AVL) is short and broad, being 1,35 times as wide as long in the smallest individuals and 1,25 times as wide as long in the

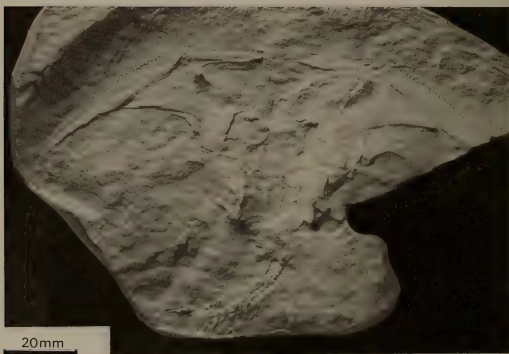


Fig. 1. *Barrydalaspis theroni* gen. et sp. nov. Silicone cast of holotype showing ventral thoracic armour in external view.

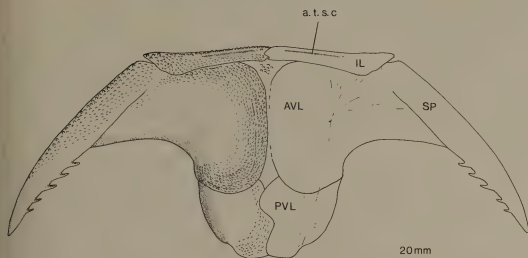


Fig. 2. *Barrydalaspis theroni* gen. et sp. nov. Restoration of the ventral thoracic armour in ventral view. Based on SAM-K4647 and K4649. AVL—anterior ventrolateral, IL—interolateral, PVL—posterior ventrolateral, SP—spinal, a.t.s.c.—anterior transverse sulcus.

larger (presumably older) individuals. With this change in linear dimensions there is also a change in shape, the posterior area of the AVL becoming squarer with increasing size (cf. Figs 1 and 2). The length of the spinal margin, expressed as a percentage of the maximum width of the plate, also varies from 48 per cent in the small individuals to 44 per cent in the large specimens. A similar decrease in the relative length of the spinal margin has been recorded for *Coccosteus* by Miles & Westoll (1968: 433–434). There is a well-marked 'Ventrolateralkante' (Gross 1933) running longitudinally on the posterior part of the AVL and across the posterior ventrolateral. This implies that there was a narrow subpectoral wall of the flank armour and the development of a postbrachial lamina. The centre of radiation of the AVL lies remarkably far forwards, more so than in any of the 'dolichothoracid' types figured by Denison (1958, fig. 112). The ornament on the AVL consists of simple tubercles which are very small at the radiation centre but become larger along the anterior, median and posterior margins. Ornament is absent from that part of the plate adjacent to the subpectoral emargination. A similar lack of ornament is noted by Miles & Westoll (1968) in the corresponding area of *Coccosteus*.

The visceral surface of the AVL shows that perichondral bone lined the scapulocoracoid. Impressions left by this perichondral layer suggest that the abdominal division and the coracoid process of the scapulocoracoid (terminology of Stensiö 1959) were both very broad, as in most 'dolichothoracids'. In some specimens the contact faces with the anterolateral can be seen, suggesting that the width of the pectoral fenestra is equal to about half the length of the subpectoral emargination.

The posterior ventrolateral (PVL) is a little longer than broad and, as usual, the left PVL overlaps the right. As mentioned above, there is a strongly

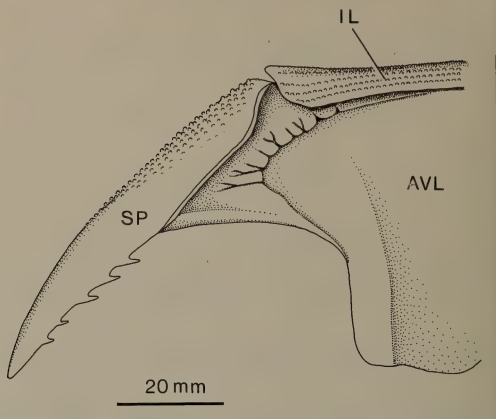


Fig. 3. *Barrydalaspis theroni* gen. et sp. nov. Restoration of anterior ventrolateral, interolateral and spinal of the left side in visceral view. Based on SAM-K4779, K4770, K4791 and K4771. Abbreviations as in Fig. 1.

developed 'Ventrolateralkante' which divides the plate into lateral (vertical) and ventral (horizontal) laminae. The lateral lamina, which is relatively long, suggests that the postbrachial lamina was also long, as in phlyctaenaspids (Denison 1958: 534). The ornament is similar to that on the AVL. The medial margin of the left PVL is 'S'-shaped where it overlaps the right but there is no indication of the complex overlap relations seen in *Tiaraspis* and *Romundina*.

The spinal (SP) is relatively long and the proportions agree more with those of Denison's phlyctaenaspid genera than with those of any other arthrodire group. The spinals are relatively longer in smaller individuals. A suture between the SP and AVL can be traced except anteriorly. As mentioned in the diagnosis, the SP is set at a very divergent angle, this being approximately 50° . *Phlyctaenius acadica* also shows a spinal set at a high angle (about 48° from the restoration given by Heintz 1934), but in this species the SP is much shorter. The ornament consists of well-developed tubercles along the lateral edge of the anterior two-thirds. Smaller tubercles are also present over half of the ventral surface and about one-fifth of the dorsal surface. Posteriorly, the medial edge bears six to eight recurved denticles.

The interolateral (IL) is orientated almost transversely and has ventral (external) and dorsal (internal or postbrachial) laminae which both become wider laterally. On the ventral lamina there is a shallow sulcus between two rows of tubercles. This sulcus, which has been variously named in arthrodires ('anterior ventral sulcus'—Miles & Westoll 1968; anterior transverse sensory canal—Mark-Kurik 1973; Orvig 1975), implies that there was a neuromast line as in *Actinolepis* and several brachythoracids. The ventral surface of the IL is covered with tubercles, similar to those on the edges of the AVL. The tubercles on the dorsal surface are regularly arranged into four or five rows. The presence of an anterior median ventral is seen in SAM-K4649 where there is the impression of tubercles between the IL and the AVL of either side. However, the shape of this plate and the existence of a posterior median ventral cannot be demonstrated in this material.

An anterolateral (AL) has not been found associated with the ventral armour, but two specimens showing most of this plate can be referred to *Barrydalaspis* because they show ornament similar to that on the AVL. A note of caution must be introduced when associating plates by using similarities in ornament. White (1969: 303) has pointed out that in *Heightingtonaspis anglica* Traquair the ornament on the AL may differ considerably from that on the AVL. However, in the South African material there are only two types of AL present, each with ornament which matches that on one or the other of the two types of ventral armour. Thus, the criterion of association by ornament seems the most reasonable with the available material.

The AL is tall and relatively narrow, similar proportions being seen only among 'dolichothoracids' in the arctolepid described by Miles (1965). As usual the bone is raised to a focal point, which in this case is centrally placed, and from this four ridges run to the corners to divide the bone into quadrants. The posterodorsal corner is produced as in *Arctolepis decipiens* Woodward and, to some extent, in *Neophlyctaenius sherwoodi* (Denison). The pectoral emargination is very wide, matching that of the AVL. Tubercles are present on the dorsal, anterior and posterior quadrants but they are very sparse on the ventral quadrant.

The anterior dorsolateral (ADL) is known from two specimens, one of which (SAM-K4648) shows part of the trunk armour preserved in lateral view. This specimen can be associated with the holotype because of the similarity of ornament and the fact that there is evidence of scales on the body. Among the 'dolichothoracids' the ADL of *Barrydalaspis* resembles that of *Tiaraspis*. Both are tall and narrow and have a dorsal margin which slopes posterodorsally and have the anteroventral angle produced. This last feature is also seen in *Neophlyctaenius sherwoodi* (Denison 1950, fig. 2). The bone is divided into lateral and dorsolateral faces by a prominent ridge below which runs the lateral line canal. A small trochlear is developed on the anteromesial edge, immediately in front of where the ridge and lateral line converge. Beneath the trochlear the anterior margin is swollen to resemble an obstantic process, but

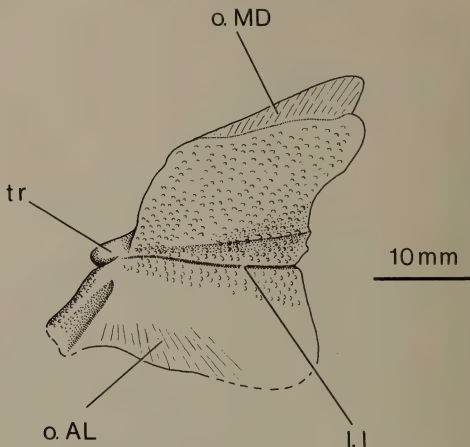


Fig. 4. *Barrydalaspis theroni* gen. et sp. nov. Restoration of anterior dorsolateral of left side. Based on SAM-K4648. l.l—lateral line, o. AL—area overlapped by anterolateral, o. MD—area overlapped by median dorsal, tr—trochlear.

it is impossible to determine if an articular face was present. The lateral face of the anteroventral corner is marked by a prominent groove. This is a feature usually found in brachythoracid arthrodires where it receives the dorsal part of the postbranchial lamina. The presence of this groove thus suggests that the dorsal part of the AL may have been inturned. The surface of the ADL is ornamented with tubercles which become larger along the posterior margin and along the crest of the ridge. The centre of radiation is found at the base of the trochlear.

One specimen (SAM-K4648) shows evidence of a posterior dorsolateral but, apart from noting the fact that it is a large plate, it is too incomplete to merit further comment. A relatively large plate is significant in showing that the lateral face of the trunk armour is not 'reduced' as it is in many brachythoracids.

The holotype and SAM-4643 show impressions of scales behind the trunk armour. The latter specimen shows that the scales are moderately large, deeper than long and completely cover at least 10 cm of the body. The scales immedi-

ately behind the posterior dorsolateral plate are deeper than those above or below and in this respect the squamation is similar to that seen in *Sigaspis* Goujet (1973, fig. 3a). There are impressions of dorsal ridge scales but no further details of these or the flank scales can be established.

Relationships of Barrydalspis

The interrelationships of the arthrodire groups have recently been reviewed by Miles (1973) and Miles & Young (1977) and some rational outline of arthrodire phylogeny has been proposed. Within the cladistic framework provided by these authors, *Barrydalspis* is to be regarded as a phlyctaenioid arthrodire by virtue of the possession of a 'ball and socket' dermal neck joint. Unfortunately, the relationships of *Barrydalspis* cannot be considered further due to lack of information about the head and the median dorsal plate. The suborder Phlyctaenioidei of Miles contains the collateral infraorders Phlyctaenii and Brachythoracii. The latter can be shown to be monophyletic (Miles 1973) based on synapomorphies in features of the head and the median dorsal plate. The former, as Miles admits, is possibly a grade group. In other words monophyly has not yet been demonstrated for the Phlyctaenii (families Tiaraspidae, Groenlandaspididae, Phlyctaenaspididae, Williamaspididae and the genus *Aggeraspis*) and more rigorous analysis of the species included within the Phlyctaenii is necessary. Some recent work suggests that *Tiaraspis* and *Groenlandaspis* may be sister groups based on the synapomorphies of a high median dorsal plate and the fact that the lateral line, in crossing the posterior dorsolateral describes a sharp dorsal flexure. These two genera, plus an unnamed form from the Middle Devonian of Australia, are included in the Groenlandaspididae by Ritchie (1975).

Thus to place *Barrydalspis* as Suborder Phlyctaenioidei incertae sedis means that it shows the synapomorphy of that Suborder but that the material does not allow us to specify its position within that group. *Barrydalspis* resembles some members of the Brachythoracii in showing a prominent groove on the ADL to receive the AL but it is not yet clear whether this should be regarded as a synapomorphy of the brachythoracids or as a feature primitive for the Phlyctaenioidei.

'Phlyctaenaspid arthrodire'

The second type of placoderm which is recognizable in the present collection is known from ventral views of the trunk armour and a partial AL which is associated with the ventral plate because of the similarity of the ornament. This arthrodire is distinct from *Barrydalspis* in a number of respects: the ventral armour of the trunk is much longer and narrower; the SP is set at a much lower angle (i.e. it is more nearly parallel to the sagittal plane) and lacks the medial denticles; the SP appears to be fused with the AVL throughout its length; the lateral end of the IL is swollen to produce what is here termed an 'elbow'; the ornament consists of coarse tubercles along the outer edge of the SP and IL

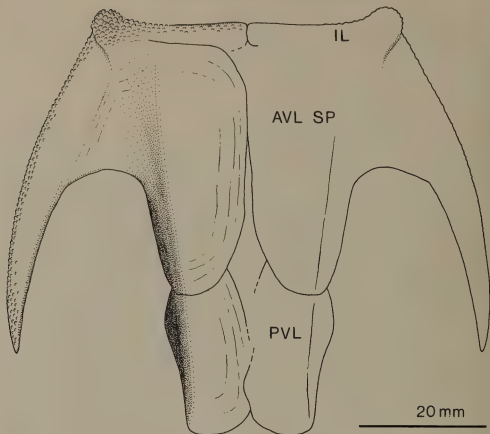


Fig. 5. 'Phlyctaenaspis arthrodire'. Restoration of ventral thoracic armour in ventral view. Based on SAM-K4640. Abbreviations as in Fig. 1.

but elsewhere is represented by minute tubercles.

The proportions and shape of the ventral armour are similar to both *Neophlyctaenius sherwoodi* (Denison 1950) and *Gaspeaspis* Pageau (1969). The former is from the late Middle or early Upper Devonian of New York State, the latter from the early Middle Devonian of Gaspé Peninsula, Quebec. As in *Gaspeaspis*, the South African form shows AVLs which meet one another in the mid-line, leaving only small areas for the anterior and posterior median ventrals (these were not seen in the South African form). The 'Ventrolateral-kante' is well developed and there was probably a long postbrachial lamina. The South African phlyctaenaspid differs from both *N. sherwoodi* and *Gaspeaspis* in the relatively longer AVL and the fusion of that plate with the SP. The division between the IL and SP is recognized as a deep groove. The prominent elbow of the IL is matched elsewhere in the Lower Devonian phlyctaenaspid *Dicksonosteus* (see Goujet 1975, pl. 4 (fig. 1)). An incomplete AL (SAM-K4775) which can be referred to the ventral armour is tall with a wide pectoral emargination and a focal point which is situated ventral to the centre of the bone. Distinctively the dorsal margin slopes anteroventrally towards the front. This last feature is

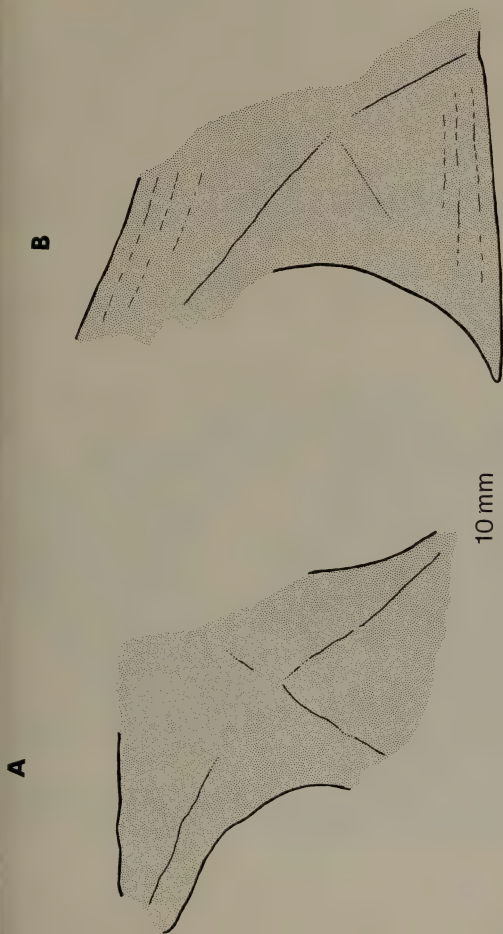


Fig. 6. A. Anterolateral plate of right side of *Barrydalaspis theroni* gen. et sp. nov. Camera lucida drawing of SAM-K4650
B. Anterolateral plate of 'phlyctaenaspis arthrodire'. Camera lucida drawing of SAM-K4775.

rare among arthrodires but is seen in species currently referred to *Phlyctaenaspis* and in *Arctolepis decipiens* (see illustrations in White 1969, figs 2-21).

In summary, this South African form is considered to be a phlyctaenaspid because it lacks the anteroventrals (a derived feature of actinolepoids (Miles & Young 1977)) and because it shows phenetic resemblances in the proportions of the ventral thoracic armour and constituent plates to certain phlyctaenaspid genera.

Arthrodire head

One specimen (SAM-K4748) shows the matrix impression of the under-surface of a partial skull roof. It cannot be associated with either of the two types described above although it is of a size that would match either. Further-

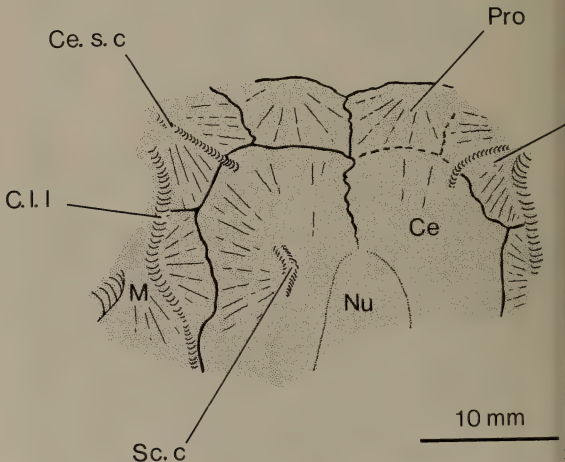


Fig. 7. Arthrodire head. Camera lucida drawing of internal cast of a partial skull roof, SAM-K4748. Ce—central, M—marginal, Nu—nuchal, Po—postorbital, Pro—preorbital, Sc.c—impression left by semicircular canals, Ce.s.c.—central sensory canal, Cl.I—cephalic division of the main lateral line.

more, it cannot be assumed that the pattern of sutures visible on the under-surface of the skull roof corresponds faithfully to that on the upper surface, which is the surface most frequently studied. For these reasons our remarks about this specimen must be limited.

The anterior end of the nuchal is narrow, gently rounded and reaches a considerable distance between the centrals. The postorbital is short and broad with the posterior margin orientated transversely. These features are seen in combination in *Gaspeaspis* (Pageau 1969, fig. 20). The marginal has a broad area of contact with the central, a feature rarely seen in actinolepoids but common in phlyctaenaspids, *Groenlandaspis* and *Aggeraspis*. What little that can be seen of the paths of the sensory canals agrees with that expected in a 'dolichothoracid'.

Undetermined arthrodire

In the collection there is one specimen (SAM-K4646, Fig. 8A) of a large arthrodire which shows coarse ornamentation unlike the forms already described

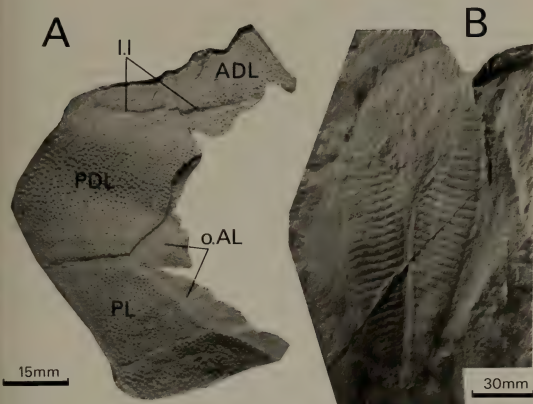


Fig. 8. A. Silicone mould of the right side of part of the trunk armour of a large arthrodire, SAM-K4646. ADL—anterior dorsolateral, PDL—posterior dorsolateral, PL—postero-lateral, l.l—lateral line, o.AL—overlap area for anterolateral.

B. ?Chimaeroid egg case. Silicone mould of SAM-K4814.

from this locality. If we have interpreted this specimen correctly, this represents an impression of the posterior part of the flank of trunk armour displaying parts of the anterior dorsolateral, posterior dorsolateral and posterolateral. The anteroventral margin of the ADL and the anterior margin of the PL are similar to those in *Groenlandaspis antarcticus* Ritchie (1975). Gavin Young (pers. comm.) suggests that the size and pattern of ornament shown in this specimen is similar to the ornamentation seen in the Antarctic *Groenlandaspis*. However, it is to be admitted that similarity in ornament is a weak basis for associating this single South African specimen with the Antarctic *Groenlandaspis* and in consequence this specimen is left unnamed.

?CHIMAEROID

There is, in the collection, a specimen of an egg capsule (Fig. 8B), 160 mm in length and with approximately thirty-two unbranched narrow transverse ridges in each lateral flange.

The egg capsules of living chimaeroids are leathery, bilaterally symmetrical and elliptical in outline. They possess a membranous lateral web, which may be strengthened by simple or branched, rib-like thickenings and the margin of which can be fimbriate or entire.

Presumably by analogy with these Recent types, some eleven fossil chimaeroid eggs have been described. The earliest descriptions are of forms from the Middle Jurassic of Germany (Bessels 1869; Jaekel 1901) while the majority of later finds have been those from the Upper Cretaceous (Gill 1905; Dean 1909; Brown 1946; Voronets 1952; Vakhrameev & Pushcharovskii 1954; Obruchev 1967). Additional material has been described from the Jurassic of Canada (Warren 1947) and the Oligocene of the U.S.A. (Brown 1946). A rather differently shaped form, almost butterfly-like, has been recorded from the Triassic of Connecticut (Bock 1949) but this is possibly a pteropod.

Thus the find reported here takes the known occurrence of these supposed egg capsules back into the Devonian. In this respect it is interesting to note that the Chimaeroidei extend back only to the Jurassic (Toarcian) although members of the Menaspoidei first occur in the Upper Devonian (Patterson 1967). If, however, pelvic claspers are a primitive feature of the elasmobranchiomorphs, as is suggested by their presence in ptyctodonts, then it is reasonable to assume that placoderms also produced egg cases (Patterson 1965) and that the egg case reported above may be that of a placoderm.

ACANTHODIAN

A specimen of an incomplete pectoral spine of *Gyracanthides* (Fig. 9) is present in the collection. The spine is flattened and is deeply grooved along the medial edge of the posterior half. The upper and lower surfaces are marked with tuberculated ribs which pass obliquely across the surface and meet in a chevron pattern along the free edge. A prominent ridge runs the length of this free edge.

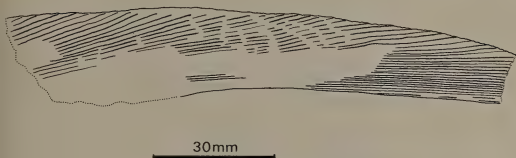


Fig. 9. *Gyracanthides* sp. Pectoral spine. Freehand sketch of rubber latex cast.

Gyracanthides is known by two species, *G. murrayi* (Woodward 1906), from the Mansfield Slate of Victoria, Australia, and *G. warreni* White (1968) from the Aztec Siltstone of Victoria Land, Antarctica. The latter is known only from two specimens representing part of the base of a pectoral spine, perhaps of the same individual (White 1968).

The South African *Gyracanthides* is similar to *G. warreni* in a number of biometric details. In both, the ribs and alternating grooves are of equal width; the ribs are almost straight; there are nine to ten ribs per cm at the base of the insertion area and thirteen to fifteen just behind this level (these counts are taken by placing a cm scale at 90° to the direction of ribbing) and the tubercles on the ribs are very closely packed. Thus, the South African *Gyracanthides* and *G. warreni* are similar in all features in which the two can be compared and there is every reason to regard them as being conspecific. *Gyracanthides murrayi* differs from *G. warreni* in that the pectoral spine and the ribs are more strongly curved and the ribs are spaced further apart, as are the tubercles upon the ribs.

THE PLANT REMAINS

The plants associated with the fish fauna consist of various types of lycopods, preserved either as 'external moulds' ('impressions'), or in some cases as matrix infillings of the cortical cavity within the stem ('endocortical casts'). Before describing the fossils, this form of preservation must be briefly reviewed.

Available for study were a number of latex casts prepared from moulds in the original matrix in South Africa, and sent to London. There was also a rather smaller number of specimens on the rock matrix, where this had been sent to London for study of the associated fish. From these, additional casts were made in latex or silicone rubber.

The lycopods represented evidently had a relatively tough cortical cylinder (Fig. 10A) within which (by analogy with Palaeozoic lycopods preserved uncompressed, as petrifications) a small stele (circle in that figure) was surrounded by a broader middle cortical cavity. As the fragmented stems became buried in matrix, this cavity became filled with mud (with or without the stellar woody cylinder at the centre).

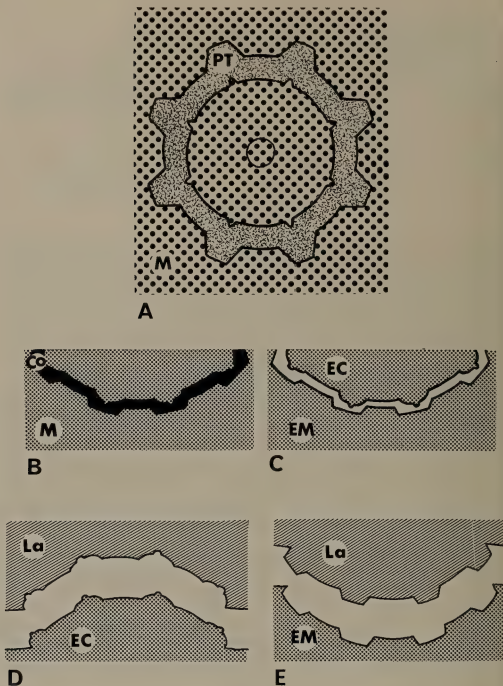


Fig. 10. Compression of stem of a lycopod such as *Archaeosigillaria*, producing the two types of fossil, endocortical cast (EC) and the external mould (EM). A. Stem lying horizontally in matrix (M). Matrix both surrounds it and fills the cortical cavity. The stem outer surface shows protruding leaf cushions; the only features on the cortical inner surface are indentations corresponding to the position of the passage of a vascular trace into the cortex. The positions of these indentations will correspond to the position of the leaf cushion. B. Compressed matrix (M) and coaly matter of the plant (Co). (The lower half only is shown.) On the outer surface protrusion of the leaf cushions is reduced with little distortion of their horizontal dimensions. The greater compressibility of plant tissue as against matrix caused collapse of

On compression, with resulting collapse of the plant tissue, the matrix filling the cortical cavity became compressed to a rod of matrix of ellipsoidal cross-section (Fig. 10B). In all cases studied, the plant material was missing, being represented either by a gap (white region in Fig. 10C), or by a dark brown (iron-rich?) porous mineral substance. The surface of an endocortical cast (EC in Fig. 10C) of such a fossil is revealed by a fracture plane passing between the cast and the enclosing matrix, i.e. the external mould. It generally shows (Fig. 14E) a topography dependent partly on any indentations on the inner surface of the cortex (e.g. passage of leaf trace, etc.) and partly on the collapse of the plant material on compression into features (e.g. leaf cushions) on the stem outer surface. Endocortical casts in this material typically show several series of longitudinal rows of bosses (Figs 12E, 14E) which correspond to the positions of leaf cushions on the original stem outer surface. They may show a small central protrusion which was a depression on the inner face of the cortex (EC in Fig. 10C). Latex 'moulds' were prepared (La in Fig. 10D) from such endocortical casts. It must be emphasized that the topography of these endocortical casts corresponds only in the broadest way to the original external appearance of the stem.

The external mould (or impression in the matrix) of the original outer surface shows a closer approximation to the original appearance of the stem. External features (e.g. leaf cushions, represented symbolically by ridges in Fig. 10A) appear in somewhat reduced topography, on such an external mould (EM in Fig. 10E). Latex casts (La in Fig. 10E), approximating to the original outer surface of the plant, may be prepared from such a mould (e.g. Fig. 13A-B).

Where leaves were still attached to such a stem, evidence of their presence is normally seen on an external mould. Where a leaf has a broad expanded base (leaf cushion) the leaf plus cushion became compressed on the upper and lower surfaces of the cylindrical stem. Such a leaf is shown in Figure 11A as though lying on the lower surface of a stem. On compression and subsequent removal (by weathering or diagenesis) of the plant material the leaf cushion is represented in the external mould by a depression in the matrix (Fig. 11C). At the bottom of this depression a narrow slit extends into the rock matrix representing the site of the lamina of the leaf. When latex is poured on to such a mould, the shape and topography of the leaf cushion are shown faithfully, but usually the latex (La in Fig. 11D), does not penetrate into the narrow mould of the

the matrix filling the endocortical cavity into the area behind the leaf cushions. The matrix forming the endocortical cast now also shows raised bosses, corresponding to the positions of leaf cushions. C. Subsequently some, or all, of the coaly matter is removed leaving the two matrix surfaces, the endocortical cast (EC) and the external mould (EM). D. Upper half of the endocortical cast (EC) exposed by fracture plane passing over cast surface, together with latex mould (La) prepared from it, a negative version of the cortical cavity (a plaster cast taken from this mould will correspond to the original endocortical cast). E. Latex cast (La) of the external mould (EM), corresponding to the original (compressed) stem surface with protruding leaf cushions.

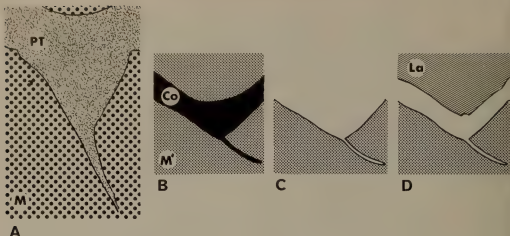


Fig. 11. *Archaeosigillaria plumsteadiae* sp. nov. Compression of leaf and leaf cushion resulting in the production, in the latex mould, of a leaf cushion showing only the 'false leaf scar'. A. Original shape of leaf and cushion (as seen in profile at edge of stem in Figs 12C, 13B), surrounded by uncompressed matrix (M) which also fills the endocortical cavity; the leaf lies in the matrix as on the lower surface of a horizontal stem. PT—plant tissue. B. Compression distorts the shape of both leaf base and leaf. The leaf cushion becomes less protruding, the thickness of the leaf lamina is reduced and its angle of emergence is decreased. Co—coaly matter. C. Removal of coaly matter (by subsequent diagenesis or weathering) gives a negative impression of the leaf cushion with a narrow mould of the leaf lamina going down into the matrix. D. Latex (La) applied to this negative mould fails to penetrate the narrow mould of the leaf lamina, leaving a 'false leaf scar' on the (positive) cast of the leaf cushion (Fig. 13A–B, f.l.s. in Fig. 12D).

leaf itself. As a result, the leaf cushion, seen (as a protruding 'positive' feature) on the latex cast prepared from this mould, does not show the leaf but merely a transverse marking—a kind of 'false leaf scar'—in the middle of the cushion (f.l.s. in Fig. 12D) where the latex failed to flow into the narrow space representing the leaf. In such a specimen the leaf may be seen in profile at one or both margins of the compressed stem (Fig. 12C; see left side of Fig. 13B).

In one specimen of *Archaeosigillaria* cf. *picosensis* the narrow mould of the leaf itself was wide enough to allow latex to enter, so producing a somewhat flattened replica of the original leaves attached to the leaf cushion surface (Figs 12A–B, 14A, F).

Although, in what is said above, the distinction is made between an endocortical cast and the external mould, the former may be encountered lying, in effect, within the latter (Fig. 14B). In this case, the visible surface features are those of the endocortical cast, but the leaves may be seen in profile at the margin (Fig. 14C–D). Unfortunately, there were no cases of 'part-and-counterpart' specimens, where external mould and endocortical cast could be seen on opposed, fractured, faces of matrix.

Two well-defined taxa of lycopods may be recognized in this material;

one is made the basis of a new species and the other is compared with a South American species. Two further kinds of rather less satisfactory lycopod fossils are also described.

Division TRACHEOPHYTA

Class LYCOPSIDA

Order PROTOLEPIDODENDRALES

Family *Archaeosigillariaceae*

Genus *Archaeosigillaria* Kidston

Archaeosigillaria plumsteadiae sp. nov.

(Figs 12C–D, 13A–B)

Etymology

Named after Dr Edna Plumstead who has contributed so much to our knowledge of South African Palaeozoic plants.

Holotype

185B, external mould (Fig. 13A).

Paratypes

161, 190A, 192A, 175. Silicone and rubber casts from the type material, two natural external moulds, are shown in Figure 13A–B.

Diagnosis

Fragments of lycopod leafy stems up to 1,5 cm diameter and 11 cm in length, represented by external moulds. Stem surface completely covered by hexagonal cushions, each typically 6,5 mm wide by 4 mm high, upper and lower edges of leaf cushions flat and in contact with cushions above and below. Cushions arranged in vertical ranks with corresponding orthostichies in alternating series. Leaves seen only in profile at margin of flattened stem mould; free part of leaf typically 6 mm long, leaving stem at about 45° and diverging from it, the apical part of the leaf being almost perpendicular to the stem. Shape of lamina otherwise unknown, but evidently not thicker than 1 mm. No evidence of leaf abscission nor of ligule or ligule pit.

Remarks

As indicated above, the shape of the leaf lamina may be seen in profile at the edges of the compressed stem (Fig. 13A, left-hand side) but over the stem surface the leaves (represented by cavities in the matrix of the fossil) cannot be seen (Fig. 11D). The latex poured into this natural mould evidently failed to flow into these cavities. Thus the only clear feature on each hexagonal leaf cushion is a transverse line at the widest part of the cushion (f.l.s. in Fig. 12D). This is rather comparable to the 'false leaf scar' of a lycopod compression

fossil when a fracture plane has detached the leaf in the counterpart fossil (cf. Chaloner & Boureau 1967: 533). It must be borne in mind that whatever is seen of the leaf lamina in profile at the flattened stem margin (Figs 12C, 13B) is only a minimum length. It may actually have been longer, depending on the shape and taper of the leaf (cf. Lacey 1962, fig. 12A, D). There is no evidence of

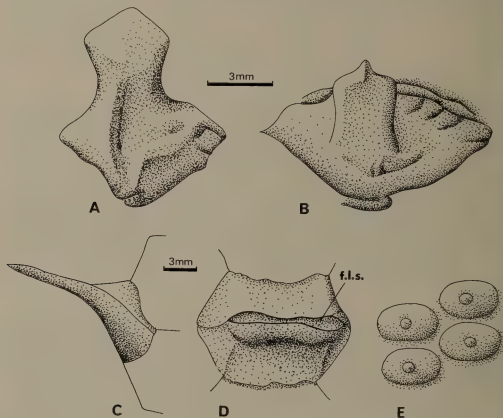


Fig. 12. *Archaeosigillaria* and 'lycopod endocortical cast'.

A-D. Leaves and leaf bases of both species of *Archaeosigillaria*. Drawn from photographs of the latex cast. A-B. *Archaeosigillaria* sp. cf. *A. picosensis* Kräusel & Dolianiti. A. Rhomboidal leaf cushion with leaf attached, 2 mm long, probably complete, lying parallel to the stem surface, with its sides tapering abruptly to form a spatulate tip; SAM-K4785. B. Another leaf cushion, with a small tab-like and probably incomplete leaf emerging from the centre of the leaf cushion; SAM-K4785. C-D. *Archaeosigillaria plumsteadiae* sp. nov. C. Leaf seen in profile at side of stem, showing uncompressed dimensions of leaf cushion, and thickness of leaf lamina (as in Fig. 11A). Leaf emerging at 45° and diverging from the stem to become nearly perpendicular to it; 190A. D. Leaf cushion of holotype (as in Fig. 13A). Hexagonal, strongly protruding leaf cushion, featureless apart from the false leaf scar (f.l.s.), a transverse line at the widest part of the cushion; 185B.

E. 'Lycopod endocortical cast' with bosses on the surface produced by processes of compression and collapse explained in Figure 10. The bulge in the centre of each boss is interpreted as a feature produced by the site of passage of the leaf trace into the cortex.

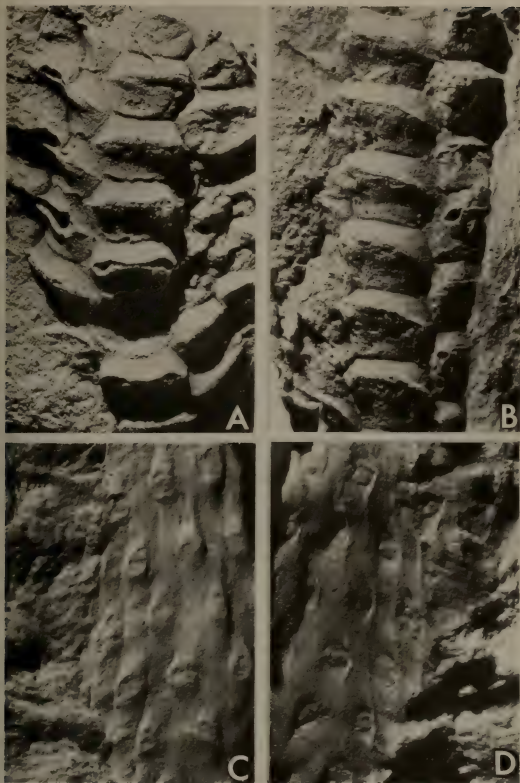


Fig. 13. A-B. *Archaeosigillaria plumsteadiae* sp. nov. Latex casts coated with ammonium chloride and illuminated from top left. A. Holotype, 185B. Stem showing three rows of contiguous hexagonal leaf cushions. $\times 3$. B. Paratype, 161. $\times 3$. Both specimens showing leaves in profile on the left.

C-D. Lycopod ?endocortical cast, cf. *Haplostigma irregulare* Seward. Illuminated from top left. SAM-K4744. C. Plaster cast prepared from latex mould, representing the original rock surface, showing circular raised features corresponding to positions of leaf bases. $\times 3$. D. Latex mould showing positions of leaf bases as depressions. $\times 3$.

leaf shedding (abscission) in these specimens; none shows a leaf scar, and hence no parichnos or vascular scar could have been represented. There is no evidence of a ligule. One specimen shows several missing leaf bases (Fig. 13A, bottom and right of specimen). The most probable explanation of this is that secondary growth of the cortex caused eventual sloughing off of the whole leaf cushions, as in the case of *Sigillaria* (Chaloner & Collinson 1975).

Grierson & Banks (1963), in their emended generic diagnosis of *Archaeosigillaria* (which the authors generally follow), do not regard this genus as having leaf cushions, and refer only to 'enlarged leaf bases becoming hexagonal on larger stems'. Their figure of the leaf of *A. vanuxemi* in profile (their pl. 35 (fig. 4)) conforms closely with that seen in our specimens. They further state (Grierson & Banks 1963: 239) that the leaves of their plant 'were persistent and that the six-sided leaf bases cannot be regarded as true cushions from which the leaf abscised but rather as merely the enlarged base of the leaf'. The authors prefer to follow the broader concept of a leaf cushion developed by Meyen (1976) and regard the swollen leaf bases of their plant as constituting cushions even though the leaf was not abscised, and would emphasize that they differ from Grierson & Banks only in terminology, and not in interpretation of their plant.

The broad leaf cushions of the present species with flat upper and lower faces in contact with cushions above and below are reminiscent of some Upper Carboniferous *Sigillaria* species, particularly those of the *Favularia* group (e.g. *S. elegans* Brongniart, particularly the specimens figured as *S. hexagona* Brongniart, a synonym of the former species). However, of course, *Archaeosigillaria plumsteadiae* differs from all *Sigillaria* species in having no indication of leaf abscission. The appearance of the leaf cushions and the profile view of the leaves in the present species are most closely matched in *Archaeosigillaria kidstoni* where the much smaller leafy shoots show comparable hexagonal leaf cushions (Lacey 1962, fig. 12B-C; Chaloner & Boureau 1967).

Archaeosigillaria plumsteadiae shows good general agreement with several species of *Archaeosigillaria* including *A. vanuxemi*, *A. kidstoni*, and with the Ghanaian *A. essiponensis* (Mensah & Chaloner 1971). It is noteworthy that these are all Lower Carboniferous species.

Comparison with *A. caespitosa* (Schwartz) Plumstead from the Witteberg is limited, as the holotype of this species is apparently an endocortical cast (Plumstead 1967, pl. 11 (fig. 2)), and none of the specimens she assigns to that species shows details of leaf shape. *A. plumsteadiae* differs from all other species of the genus with hexagonal leaf cushions in their being broader than long. It must be accepted that this distinction is relatively trivial, but on available information this separates the present species consistently from earlier described ones. The authors endorse Meyen's (1976) emphasis on the need for as wide a range of specimens as possible in order to establish the extent and variability in fragments of lycopod stems. Unfortunately, as here, such a range is not always available.

Archaeosigillaria sp. cf. *A. picosensis* Kräusel & Dolianiti
(Figs 12A–B, 14A, F–G)

Material

SAM-K4785 (Fig. 12A, B; Fig. 14A, F), 'D' (Fig. 14G), SAM-K4650.

Description

This species is represented by several specimens showing fragments of stem outer surface, seen only as a natural mould (i.e. a negative version of the original stem surface) in the matrix. The stem surface is formed of contiguous rhomboidal to rounded-rhomboidal leaf cushions (expanded leaf bases), typically 4 mm wide by 2.5 mm high, arranged in prominent alternating vertical series. Arrangement of the cushions must have been either in alternating whorls or a very low angle spiral. The leaves were still in attachment, the free portion being about 1 mm wide and 2 mm long.

Remarks

No leaves are seen in profile at the edges of the specimens as in the last species, perhaps because they represent fragments of a larger stem rather than parts of a complete cylinder. However, latex evidently penetrated the leaf cavities in the mould more freely than in *A. plumsteadiae* (possibly due to greater thickness of the leaves) so that something of the form of the leaves is seen in the latex cast of the stem prepared from the mould (Figs 12A–B, 14A, F). This can be compared with the situation in *A. conferta* (Menendez 1965) where leaves are seen on the surface because the fracture plane exposing the fossil followed the plane of the leaf laminae rather than the stem surface. It is possible that these small tab-like leaves (seen in the latex casts) represent incomplete infill by the latex of a larger leaf cavity, or possibly the original leaf shape was somewhat eroded before fossilization. It is interesting to compare the situation here with that in *A. plumsteadiae*, where the latex did not penetrate the leaf cavity. On one of the specimens (Fig. 14G) there is evidence of secondary cortical growth resulting in the lateral separation of the leaf bases revealing (?) cortical tissue between them. This is, of course, a common phenomenon in many *Lepidodendron* species (Thomas 1966).

In the leaf shape and arrangement this material agrees well with those species of *Archaeosigillaria* seen to have short tab-like leaves turning abruptly from the leaf cushion to parallel the stem surface or lie obliquely to it; these include *A. vanuxemi*, *A. kidstoni*, and *A. essiponensis*, with leaves showing at the side of the stem, and more particularly *A. picosensis*. This plant, from the Picos member in Brazil (Lower Devonian according to Kräusel & Dolianiti 1957), is preserved like the specimens here as a natural mould with leaves showing on the surface and is the closest species to the Bokkeveld plant. Those authors describe their specimen (free translation from the German summary) as 'small stems, [covered with] leaf cushions pressed together, rounded-angular to rhomboidal, also in part hexagonal, bearing in their upper part a small

thin leaf' (literally, leaflet). It should be noted that the age of Kräusel & Dolianiti's specimen, cited by them as Lower Devonian, may well be much younger. Sampaio & Northfleet (1973) offer an age correlation for the Picos member (of the Pimenteiras Formation) as ranging between Emsian and Eifelian; Bär & Riegel (1974) favour 'Middle Devonian Age'. The age of *A. picosensis* is probably best placed only within a broad bracket between Emsian and Frasnian (Brito 1971, fig. 10).

LYCOPOD ENDOCORTICAL CASTS

(Fig. 14B-E)

Material

SAM-K4790, K4798a.

Remarks

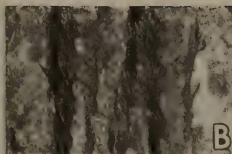
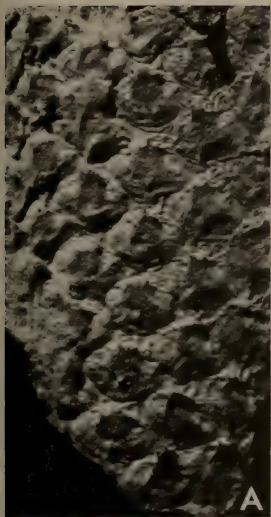
The specimen illustrated in Figure 14E is one of several in the latex casts available in which the topography of the fossil appears to represent only a very blurred version of the lycopod stem. This cannot be reconciled with leaf bases or remains of attached leaves, and this fossil is interpreted as representing an endocortical cast. This shows the positions of leaves in the form of bulges or bosses on the endocortical cast, which simulate leaf bases or cushions (EC in Figs 10C-D, 12E, 14E). One of these casts K4798a (Fig. 14B-D), besides showing these vertically seriated bosses, also shows leaves in profile along the margin. The leaves appear to be preserved in a brown mineral substance which must have come to occupy the site of the original plant tissue. This mineral matter is a thin layer on the outside of the cast, representing the cortical tissue and leaf bases of the stem. The leaves are somewhat similar to those of some species of *Archaeosigillaria*, such as *A. essiponensis* (Mensah & Chaloner 1971) and *A. kidstoni* (Lacey 1962; Chaloner & Boureau 1967), being short with a broad base and tapering towards the apex.

On the other cast SAM-K4790 (Fig. 14E) this mineral matter is not present, and on the left-hand side a cavity can be seen representing the gap between the endocortical cast and the external mould, i.e. the site of cortical

Fig. 14. A, F, G. *Archaeosigillaria* sp. cf. *A. picosensis* Kräusel and Dolianiti. A. Latex cast of a fragment of an external mould showing contiguous rhomboidal leaf bases with attached leaves, one of which, near top left, is more complete than the others; SAM-K4785. F. Scanning Electron Micrograph photograph of an area of the same specimen, taken on a Cambridge S600 at a stub angle of 10°. (Horizontal axis only, $\times 12$.) G. Latex cast showing separation of leaf bases, SAM 'D' $\times 7.5$.

B-E. Indeterminable lycopod endocortical casts. Photographs of original rock surface. B. Part of cast immersed in alcohol, photographed to show vertical files of raised bosses on the surface. At both sides there is a thin layer of mineral matter, representing the site of original plant tissue, and showing leaves in profile, one on the left-hand edge, three on the right. SAM-K4798a. $\times 3$. C-D. Detail of leaves (immersed in alcohol). Short leaves with a broad base tapering to a thin lamina, at about 45° to the stem surface. $\times 5$.

E. Cast photographed dry, lighting from top left, showing seriated raised bosses; SAM-K4790. $\times 3$.



tissue. These endocortical casts are generally comparable to those formed on the matrix infill inside *A. essiponensis* (cf. Plumstead 1967, pl. 11 (fig. 2); Mensah & Chaloner 1971, pl. 64 (fig. 7)), but other genera can produce similar casts (e.g. Plumstead 1967, pl. 15 (fig. 3) attributed to *Haplostigma*). The authors do not believe that such fossils can be assigned to genera based on characteristics of leaf cushion shape and prefer to leave these present specimens unassigned.

Lycopod ?endocortical cast, cf. *Haplostigma irregulare* Seward
(Fig. 13C-D)

Description

The specimen figured in Figure 13D (and a plaster cast prepared from that latex mould, so representing the original rock surface, Fig. 13C) shows vertically seriated round markings on a grooved stem surface, the grooves apparently separating elongated leaf cushions. This specimen is preserved as a 'positive' cast apparently showing detail of the surface topography, rather than the blurred bosses described above. It is believed that this is due to the plant possessing only a narrow zone of cortical tissue, which in compression would collapse to a uniformly thin layer more or less conforming to the stem's original external topography on both surfaces. No leaves are in evidence in the material, and it is not clear whether they were abscised. It is accordingly regarded as generically indeterminable but is figured since it shows some resemblance to the holotype of *Haplostigma irregulare* Seward, 1903, from the Bokkeveld (as refigured by Plumstead 1967, pl. 13 (fig. 3), pl. 14 (fig. 5)). It is also comparable to the specimens attributed to the same species by Kräusel (1960, fig. 88) from the Ponta Grossa Formation of Brazil.

DISCUSSION

The Bokkeveld Series consists of alternating bands of sandstone and shale which vary in number and thickness over wide areas of the Cape Province (Plumstead 1967). This is overlain conformably by the Witteberg Series. Most authors divide the Bokkeveld Series into lower and upper beds which, by reason of the contained fossils, are thought to represent marine and shallow marine/freshwater deposits respectively. One author, Swart (1950), suggests that in at least one locality shallow marine conditions persisted throughout the Bokkeveld Series. In the Barrydale area the more usual freshwater beds are clearly seen, and the fish are found in these upper beds of the Series.

The interpretation of the lower beds as representing marine conditions is well founded. A large number of marine species have been described (Lake 1904; Reed 1925 and refs; Haughton 1969) including lamellibranchs, brachiopods, trilobites, gastropods, cephalopods, corals and crinoids. A consensus of opinion holds that the lower marine beds of the Bokkeveld Series are of Lower Devonian age, and Boucot *et al.* (1967) are more precise in suggesting an Emsian age.

Further, several authors (Du Toit 1939; Doumani 1965; Haughton 1969) note the close similarity of the marine faunas of the Bokkeveld with the presumed contemporaneous strata in the Falkland Islands, Bolivia, Argentina, southern Brazil and Antarctica. Therefore, on the strength of the evidence of the underlying marine sequence, the fish- and plant-bearing beds of the Bokkeveld Series cannot be older than Middle Devonian.

The only information available here (J. N. Theron, pers. comm.) on the position of the fish fauna is that it is some '6 000 ft' below the fish zone of the Upper Witteberg (Gardiner 1969) and as such may be anything from Middle Devonian to Lower Carboniferous. At first sight the fact that the fauna contains two dolichothoracid arthrodires suggests a Lower/Middle Devonian age since the dolichothoracids reached their acme in the Emsian/Eifelian (Miles 1969). Nevertheless, *Groenlandaspis* is a widespread late Devonian representative of the dolichothoracids, while *Neophlyctaenius* survived into the Frasnian in the eastern United States (Denison 1950). Since one of the dolichothoracids is a completely new form and the other closely resembles *Phlyctaenius*, their stratigraphic significance is not apparent. Similarly, the occurrence of large arthrodire plates resembling *Groenlandaspis* does no more than confirm a Middle or Upper Devonian age. However, from the same general area as the other specimens, but not, unfortunately, as accurately located within the sequence, occurs a spine of the large acanthodian *Gyracanthides*. Elsewhere *Gyracanthides* is recorded from the Upper Devonian of Victorialand, Antarctica (White 1968) and the Lower Carboniferous of Mansfield, Australia (Woodward 1906).

The Upper Devonian Antarctic fish fauna from Victorialand is characterized by the presence of *Bothriolepis*, *Phyllolepis*, *Groenlandaspis*, holoptychiids and various acanthodians and sharks (Gavin Young pers. comm.) whereas the Australian Lower Carboniferous fauna from Mansfield has *Strepsodus*, *Ctenodus*, *Elonichthys* and three acanthodian genera but no placoderm genera. There can be little doubt that the Antarctic fauna is Upper Devonian (Young 1974) and if this South African fauna is to be interpreted as being of similar age then the absence of more typical Upper Devonian forms such as *Bothriolepis*, *Phyllolepis* and *Holoptychius* from the Bokkeveld is difficult to understand. Nevertheless the presence of a typical Lower Carboniferous fish fauna in the overlying Witteberg Series, some 1 800 m (6 000 ft) above the fish-bearing layer of the Bokkeveld convinces the authors that the fauna under discussion must be at least of Upper Devonian age and the only safe conclusion that can be drawn is that the fish fauna is Middle/Upper Devonian.

The only plants in this flora which may be of significance in dating these rocks are the two species of *Archaeosigillaria*, and in particular the very distinctive *A. plumsteadiae*. Plants belonging to this genus range from Middle Devonian to Upper Carboniferous (Banks 1960; Grierson & Banks 1963; Lejal 1970; Mensah & Chaloner 1971). Recently Lejal-Nicol (1975) has described a number of typically Middle or Upper Devonian and Lower Carboniferous lycopod

genera (including *Protolopododendron*, *Lepidodendropsis*, *Lepidosigillaria* and *Archaeosigillaria*) from Libya. Lejal-Nicol maintains that these deposits are of Lower Devonian age, and a further flora is described containing *A. kidstoni* from rocks believed to be of Pre-Siegenian age (either Gedinian or Siluro-Devonian). These genera, which are characterized by various peculiarities of their leaf cushion shape and arrangement, do not appear in Europe and North America until the Middle or Upper Devonian (Grierson & Banks 1963; Chaloner & Boureau 1967). Typical lycopods of the Lower Devonian from continents other than Africa (e.g. *Drepanophycus* and *Baragwanathia*) show no significant development of leaf base expansion comparable to the cushions of the later arborescent lycopods. Even in the Middle Devonian lycopods with a leaf cushion or cushion-like feature (e.g. *Protolopododendron*, *Leclercqia*, and *Colpodexylon*) this feature is poorly developed compared with that seen in the arborescent lycopods of the late Devonian and early Carboniferous. On this basis an extreme age bracket is put on these Bokkeveld lycopods as Middle Devonian to Lower Carboniferous, with the strongest possibility of their being Upper Devonian (Frasnian-Famennian).

It may be useful to note that shoots of lycopods such as *Archaeosigillaria* were evidently among the more robust of plant remains occurring in the Upper Palaeozoic; they commonly survived when no, or few, other plants were represented in coarse non-marine lithologies, or even in marine environments. *Archaeosigillaria kidstoni* occurs in the coral/brachiopod-rich Carboniferous Limestone in Britain (Chaloner & Boureau 1967) and the holotype of *A. vanuxemi* is closely associated with a brachiopod fauna. The present association of lycopods with fish remains is therefore not surprising.

The evidence of both the fish and the plants suggests, therefore, that these fossils come from an horizon within the Bokkeveld Series that is either Middle or Upper Devonian. Hopefully, further collecting in these strata will yield fossils giving a more precise stratigraphic position.

ACKNOWLEDGEMENTS

We should like to thank Dr J. N. Theron for bringing this material to our attention. Our thanks are also due to Drs R. S. Miles and G. C. Young for comments on the fishes, and to Dr O. Rösler and Professors H. P. Banks and J. D. Grierson for comments on South American stratigraphy and the lycopods. Finally, we thank the authorities of the South African Museum for allowing us to comment on this material.

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ADDENDUM ADDED IN PRESS

After preparing this manuscript for publication, the authors received (August 1979) an offprint of Plumstead's (1977) account of *Zosterophyllum de-vriesii* and *Z. bokkeveldensis*. (The former name is here hyphenated to give a single epithet, in accordance with the International Code of Botanical Nomenclature, Art. 23.) It is immediately evident from Plumstead's figures and specimen citations that the species described above as *Archaeosigillaria plumsteadiae* is based on the same fossil assemblage (and in part the same specimens?), from the same locality, as her *Zosterophyllum de-vriesii*. No basis in her paper is found for revising the views expressed here, that these cylindrical structures covered with closely spaced hexagonal leaf cushions represent a lycopod vegetative axis and not a zosterophyll fructification. Her photographs and her text-figure 3 (central figure) clearly show what has been here interpreted as the free tips of the leaves, seen in profile at the stem margin (her 'bisected empty sporangial sacs'). The clear validity and priority of Plumstead's specific name is acknowledged, and accordingly it is reassigned:

Archaeosigillaria de-vriesii (Plumstead) comb. nov.

Synonyms:

Zosterophyllum de vriesii Plumstead, 1977: 270, text-fig. 3, pl. 1 (figs 1-10).

Archaeosigillaria plumsteadiae Chaloner *et al.* 1979 (this paper): figs 12C-D, 13A-B.

Plumstead's *Zosterophyllum bokkeveldensis* does not appear to be strikingly distinct from *Z. de-vriesii*, but her view that they are distinct species is not challenged. It is agreed that they are congeneric (i.e. may both be placed in *Archaeosigillaria*), but no formal reassignment of the former species is suggested.

The age implication of the authors' systematic assignment of these plant fossils is, of course, at variance with Plumstead's. In rejecting assignment to *Zosterophyllum*, the suggestion of a Middle or Upper Devonian horizon rather than the Lower Devonian which was implicit in attributing these fossils to *Zosterophyllum*, is sustained.

REFERENCE

- PLUMSTEAD, E. P. 1977. A new Phytostratigraphical Devonian Zone in southern Africa which includes the first record of *Zosterophyllum*. *Trans. geol. Soc. S. Afr.* **80**: 267-277.

W. G. CHALONER
London, September 1979

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (*Lembulus*) *bicuspadata* (Gould, 1845)

Figs 14–15A

Nucula (*Leda*) *bicuspadata* Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspadata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspadata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

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In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

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Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

W. G. CHALONER F.R.S.

P. L. FOREY

B. G. GARDINER

A. J. HILL

V. T. YOUNG

DEVONIAN FISH AND PLANTS FROM THE
BOKKEVELD SERIES OF
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ANNALS

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Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

Footnotes should be avoided unless they are short and essential.

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- BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
FISCHER, P.-H. 1948. Données sur la résistance et de la vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.
FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.
KOHN, A. J. 1960a. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.
KOHN, A. J. 1960b. Spawning behaviour, egg masses and larval development in *Conus* from the Indian Ocean. *Bull. Bingham oceanogr. Coll.* 17 (4): 1-51.
THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Fischer. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume 81 Band
February 1980 Februarie
Part 4 Deel



ONTOGENY AND SEXUAL DIMORPHISM IN
AULACEPHALODON (REPTILIA,
ANOMODONTIA)

By

S. M. TOLLMAN
F. E. GRINE
&
B. D. HAHN

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

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Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na gelang van die
beskikbaarheid van stof

Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad

OUT OF PRINT/UIT DRUK

1, 2(1-3, 5-8), 3(1-2, 4-5, 8, t.-p.i.), 5(1-3, 5, 7-9),
6(1, t.-p.i.), 7(1-4), 8, 9(1-2, 7), 10(1-3),
11(1-2, 5, 7, t.-p.i.), 15(4-5), 24(2), 27, 31(1-3), 32(5), 33

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Kopieregnavrae aan die Suid-Afrikaanse Museum

ISBN 0 908407 87 4

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

ONTOGENY AND SEXUAL DIMORPHISM IN *AULACEPHALODON* (REPTILIA, ANOMODONTIA)

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(With 10 figures and 6 tables)

[MS. accepted 11 October 1979]

ABSTRACT

A large number of *Aulacephalodon* crania have been examined by means of biometrical (allometric) methods. The results of this investigation indicate that this sample represents a morphometrically homogeneous group, and that probably only a single species of *Aulacephalodon*, viz. *A. baini*, is represented in the Permian sediments of South Africa and Zambia. A qualitative analysis of nasal boss and temporal arch morphology indicates that these features are related to sexual dimorphism. Sexual dimorphism of the cranium appears to have been expressed in individuals with a basal skull length of between 190 and 245 mm. The geographical distribution of these fossils has been examined also.

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INTRODUCTION

Numerous anomodont fossils have been recovered from lower Beaufort Group sediments of South Africa. Well over 100 anomodont species have been described from *Cistecephalus* Zone strata alone. The *Cistecephalus* Zone, as defined by Kitching (1970, 1977), includes both Broom's (1906) *Endothiodon* Zone and the lower and middle portions of his *Cistecephalus* Zone. Kitching (1970, 1971) has classified the upper horizons of Broom's (1906) *Cistecephalus* Zone as the *Daptocephalus* Zone.

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Ann. S. Afr. Mus. **81** (4), 1980: 159–186, 10 figs, 6 tables.

One of the most commonly occurring forms in these sediments is a rather homogeneous group of anomodonts which have been referred to the genus *Aulacephalodon* by Houghton & Brink (1954) and Keyser (1969). The fossil remains of this reptile appear to have a rather limited stratigraphic range; in the *Cistecephalus* Zone, they occur in sediments with a vertical thickness of some 330 m, but they are concentrated in a relatively thin horizon (about 80 m) in which the zone fossil, *Cistecephalus*, occurs abundantly (Keyser 1969). *Aulacephalodon* has been recovered, albeit rarely, from within the first 3 m of the overlying *Daptocephalus* Zone (Kitching 1977), and fossils of *Aulacephalodon* have been found in comparatively large numbers at the northern (Chikonta) localities of the upper Member of the Upper Madumabisa Mudstone 'Formation', Luangwa Valley, Zambia (Drysdall & Kitching 1963).

A number of genera and species of aulacephalodonts have been described, but only a few have been based on more than fragmented fossils, and none has been diagnosed adequately. In very few instances has either ontogenetic growth or sexual dimorphism been considered in the description of a new taxon.

Owen (1844) described the first species of this group, on the basis of a single specimen, as *Dicynodon baini*. He later referred a second specimen to *D. baini* because it showed 'the same character of the tusk' as the type-species (Owen 1876). A second species, *D. tigriceps*, was described also by Owen (1855). Seeley (1898) divided *Dicynodon* into two subgenera. He proposed that those forms of *Dicynodon* which exhibit a short snout and a wide cranium be included in the subgenus *Aulacephalodon*. Broom described two further species of *Dicynodon*, viz. *D. laticeps* (Broom 1912) and *D. moschops* (Broom 1913). In 1921 he proposed a new genus, *Bainia*, for the 'tusked specimens of *Dicynodon*'; he included the species *D. baini*, *D. tigriceps* and *D. laticeps* in the genus *Bainia* and named two more species, *B. peavoti* and *B. haughtoni* (Broom 1921). Later, Broom (1932) recognized the validity of Seeley's (1898) subgeneric name *Aulacephalodon* but, as pointed out by Keyser (1969), he altered the spelling, probably as a mistake from the spelling of Seeley's (1898) other subgenus *Aulacocephalus*, to *Aulacocephalodon*. Broom considered that, '*Aulacocephalodon* . . . ought to be accepted for the group of broad skulled anomodonts typified by *Dicynodon baini* if we regard them as worthy of separate generic rank. . . . Certainly they must be placed in at least a subgenus, and I think we can quite safely regard *Aulacocephalodon* as a distinct genus. Some years ago I proposed the name *Bainia* for the large broad-headed types not fully recognising the claims of Seeley's name' (Broom 1932: 191-192).

He referred six species, namely *Dicynodon baini*, *D. tigriceps*, his own *D. laticeps*, *D. moschops*, *Bainia peavoti*, and *B. haughtoni* to the genus '*Aulacephalodon*'; and he described a new species, *A. latissimus* (Broom 1932). In the same work Broom (1932, fig. 65A-B) figured the dorsal and lateral views of an apparently nearly complete cranium with the legend, 'view of skull of *Aulacocephalodon whaitsi*, Broom'; however, there is no accompanying description which serves to define or differentiate that taxon. Accordingly, the name

Aulacocephalodon whaitsi does not satisfy Article 13 of the International Code of Zoological Nomenclature (1964) and it must, therefore, be considered as a nomen nudum. The generic name '*Aulacocephalodon*' was used subsequently by Broom (1936, 1937, 1940, 1941, 1948), Broom & George (1950), Van Hoepen (1934), and Haughton & Brink (1954). However, Keyser (1969) has pointed out that the name '*Aulacocephalodon*' is probably an incorrect subsequent spelling of Seeley's name *Aulacephalodon* and thus '*Aulacocephalodon*' has no status in nomenclature; the correct generic name is *Aulacephalodon* Seeley.

Broom (1928) described the species *Dicynodon milletti*, and Van Hoepen (1934) placed this species in *Aulacephalodon*; Keyser (1969) has referred it to *Oudenodon*, as a junior synonym of *O. bairni*, and he has noted that Broom's (1913) *Dicynodon moschops* (which Broom referred to *Aulacephalodon* as a valid species in 1932) probably represents a valid species of *Pelanomodon*.

To date some seventeen species which have been referred to *Aulacephalodon* have been described (Table 1). Keyser (1969) has examined the supposed features that have been used in the diagnosis of various *Aulacephalodon* species and has concluded that, for most of these characters, their variability and susceptibility to diagenetic distortion makes them highly questionable as taxonomic criteria. He made the important observation that, since many of the features used to distinguish the various species are to at least some extent size-dependent, the possibility that these species are all synonyms deserves consideration.

TABLE 1

List of suggested synonyms of *Aulacephalodon bairni* (Owen).

<i>Dicynodon bairni</i>	.	.	.	Owen, 1844
<i>Dicynodon tigriceps</i>	.	.	.	Owen, 1844
<i>Dicynodon laticeps</i>	.	.	.	Broom, 1912
<i>Bainia peavoti</i>	.	.	.	Broom, 1921
<i>Bainia haughtoni</i>	.	.	.	Broom, 1921
<i>Aulacephalodon latissimus</i>	.	.	.	Broom, 1932
<i>Aulacephalodon nesamanni</i>	.	.	.	Broom, 1936
<i>Aulacephalodon nodosus</i>	.	.	.	Van Hoepen, 1934
<i>Aulacephalodon luckhoffi</i>	.	.	.	Broom, 1937
<i>Aulacephalodon hartenbergi</i>	.	.	.	Broom, 1937
<i>Aulacephalodon coatonii</i>	.	.	.	Broom, 1941
<i>Aulacephalodon brodiei</i>	.	.	.	Broom, 1941
<i>Aulacephalodon cadlei</i>	.	.	.	Broom, 1948
<i>Aulacephalodon pricei</i>	.	.	.	Broom & George, 1950
<i>Aulacephalodon vanderhorsti</i>	.	.	.	Broom & George, 1950

Consequent upon Keyser's suggestion, the hypothesis entertained in this study was that many, if not all, of the *aulacephalodont* specimens which have been described possibly constitute an ontogenetic series of a single species of *Aulacephalodon*. A number of *aulocephalodont* crania were biometrically analysed in an attempt to ascertain whether an ontogenetic growth series could be demonstrated for this anomodont, and also whether the phenomenon of allometric growth could explain the supposed morphological differences between

the various proposed taxa. The possibility that sexual dimorphism was expressed in the cranium of *Aulacephalodon* (as suggested by Broom 1937, 1948; Keyser 1969) has been examined.

MATERIAL AND METHODS

Thirty-three specimens were examined. The material ranged from relatively undistorted crania to portions of the skull. The principles of relative (allometric) growth were applied to 18 of the crania (Table 2, Nos. 1–18) whilst the remainder of the specimens received less rigorous biometric treatment. Some 31 different measurements were defined (Fig. 1), but, because of the often fragmentary and distorted nature of the fossils, there were only 4 specimens for which all 31

TABLE 2

List of all specimens of *Aulacephalodon* examined in this study.

Specimen	Number	Previous taxonomic designation	Description	V	Sex
1	SAM-3328	<i>A. haughtoni</i> (T)	cranium	12	indet.
2	SAM-8747	<i>A. latissimus</i> (T)	cranium	28	female
3	SAM-K1221	<i>A. luckhoffi</i> (T)	cranium	25	female
4	BPL.FN. 1207		cranium	31	indet.
5	BPL.FN. 806	<i>A. pricei</i> (T)	cranium	31	male
6	BPL.FN. 300	<i>A. baini</i>	cranium	31	? female
7	BPL.FN. 904		cranium	26	indet.
8	BPL.FN. 4087	<i>A. baini</i>	cranium	30	female
9	BPL.FN. 4124	<i>A. cf. baini</i>	cranium	29	female
10	BPL.FN. 642	<i>A. cf. baini</i>	cranium	7	male
11	BPL.FN. 2594	<i>A. sp.</i>	cranium	14	male
12	BPL.FN. 634	<i>A. vanderhorsti</i> (T)	cranium	28	male
13	BPL.FN. 2460	<i>A. sp.</i>	cranium	31	male
14	BPL.FN. 3950	<i>A. cf. baini</i>	cranium	20	female
15	BPL.FN. 2983	<i>A. baini</i>	cranium	29	male
16	BPL.FN. 4106	<i>A. baini</i>	cranium	12	female
17	BPL.FN. 493	<i>A. baini</i>	skull	23	male
18	BPL.FN. 304	<i>A. baini</i>	cranium	29	female
19	TM 287	<i>A. hartzenbergi</i> (T)	snout	*	indet.
20	TM 1494	<i>A. brodiei</i> (T)	skull	*	female
21	TM 4043	<i>Aulacephalodon</i>	cranium	*	female
22 +	TM 4118	<i>A. sp.</i>	cranium	*	female
23 +	TM 953	? <i>Aulacephalodon</i>	occiput	*	
24 +	TM 2043	<i>A. sp.</i>	snout	*	female
25 +	TM 4471	<i>A. sp.</i>	cranium	*	indet.
26 +	TM 1506	<i>A. sp.</i>	skull	*	indet.
27 +	TM 4468	<i>A. sp.</i>	snout	*	indet.
28 +	TM 4452	<i>A. sp.</i>	cranium	*	indet.
29 +	TM 4467	<i>A. sp.</i>	cranium	*	indet.
30 +	TM 4469	<i>A. sp.</i>	cranium	*	
31	GS K30	<i>A. baini</i>	snout	*	female
32	GS R550	<i>A. baini</i>	cranium	*	male
33	GS RS415	<i>A. baini</i>	cranium	*	male

V = number of mensurable parameters recorded; * = specimens not included in the allometric analysis; + = specimens for which no locality data are available (thus, not included in Table 6); (T) = holotype; SAM = South African Museum, Cape Town; BPL.FN. = Bernard Price Institute for Palaeontological Research, Johannesburg; TM = Transvaal Museum, Pretoria; GS = Geological Survey, Pretoria.

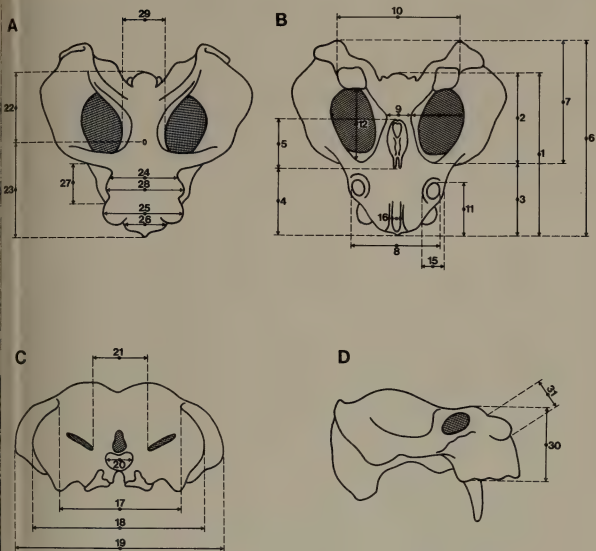


Fig 1. *Aulacephalodon* cranial measurements. A. Dorsal. B. Basal. C. Occipital. D. Lateral. 1. Basal cranial length. 2. Basal snout length. 3. Basal snout length. 4. Palatal length. 5. Pterygoid fossa length. 6. Total cranial length. 7. Temporal cranial length. 8. Bicanine breadth. 9. Least presphenoid breadth. 10. Interquadrate distance. 11. Canine-snout length. 12. Temporal fossa length. 13. Temporal fossa breadth. 14. Buccolingual diameter of canine (or socket). 15. Breadth of caniniform process. 16. Width between premaxillary ridges. 17. Least squamosal breadth. 18. Intermediate temporal breadth. 19. Greatest cranial width. 20. Breadth of occipital condyle. 21. Least post-temporal fossa breadth. 22. Post-pineal length. 23. Pre-pineal length. 24. Least interorbital width. 25. Greatest width between nasal bosses. 26. Snout width. 27. Orbital length. 28. Greatest width between prefrontal bosses. 29. Intertemporal width across pineal foramen. 30. Greatest snout length. 31. Length of nasal bosses.

metrical features could be recorded. The cranium only was measured, as the mandible is missing from most of the specimens. The variables selected for measurement were designed to reflect the overall shape of the cranium and its various parts rather than the configuration of individual bones.

All measurements were taken with either a sliding vernier caliper or the top segment of an anthropometer and were recorded to the nearest millimetre. In a number of instances, owing to either distortion or breakage of the specimen, some variables could not be measured directly. In these cases estimates of the diameters were made on the basis of symmetry in order to correct for distortion and missing fragments of bone. For those crania which were too badly distorted or broken to permit reasonable estimates, the affected measurements were not recorded.

The study of relative growth has been characterized by Gould (1966) as the analysis of size and its consequences. Allometric growth refers simply to the changes in proportion that occur as an organism increases in size. Such growth can be assessed and described quantitatively when measurements are fitted to the biparametric power function

$$y = ax^{\beta}$$

where y is a variable whose increase relative to that of another parameter, x , is considered; a is a numerical constant and β is the slope of the rectilinear plot, or, simply, the ratio of the specific growth rates of variables x and y (Huxley 1932). This approach rests on the observation that the size of an organism, and not its rate of growth, is important when one determines the proportions of its parts (Dodson 1975a). If this equation is converted to logarithms, the problem is reduced to the fitting of a straight line:

$$\log y = \log a + \beta \log x.$$

This may be rewritten as

$$Y = \alpha + \beta X$$

where $Y = \log y$, $X = \log x$ and $\alpha = \log a$. The allometric coefficient, β , is the slope of the 'best straight line' through the data, and may be considered as the value of Y when $X = 0$. Thus, β is the ratio of the specific growth rates of Y and X ; it serves as an indication of the intensity of differential size increase. Values of β greater than 1 (positive allometry) imply a differential increase of Y relative to X ; when β is less than 1 (negative allometry) the Y/X ratio decreases with an increase of the absolute magnitude of X . Isometry, when $\beta = 1$, represents the maintenance of geometrical similarity with size increase.

In determining the slope of the 'best straight line' through the data, Kermack & Haldane (1950) and Kermack (1954) have cautioned against the use of regression models which assume error to be related to only a single variable. Consequently, the fitting procedure utilized here was that of Bartlett's (1949) 'best fit'. This method was found to be the preferred procedure in a computer simulation of ten different methods by Kidwell & Chase (1967), because it (i) is highly accurate, (ii) has a small variance, (iii) has a simple procedure for setting confidence limits on the estimates, and (iv) includes a

simple linearity test. Bartlett's (1949) method has been recommended for analysis of allometric growth by Simpson *et al.* (1960) and has been so used by Dodson (1976) and Grine *et al.* (1978). A description of Bartlett's method has been provided by Grine *et al.* (1978) and will not be repeated here.

Two diameters, basal cranial length (variable 1) and basal snout length (variable 3) were utilized as comparative (x) measurements in the present study. Basal snout length was found to have a nearly isometric relationship to basal cranial length, and use of the former permitted specimens, for which the latter length was not obtainable, to be included in the analysis of sexual dimorphism.

In addition to a bivariate quantitative assessment, several qualitative features were examined in an attempt to define sexual dimorphism in *Aulacephalodon* crania.

CRANIAL GROWTH AND VARIABILITY

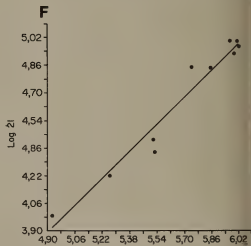
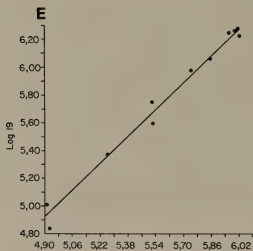
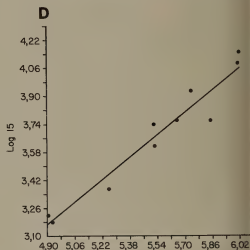
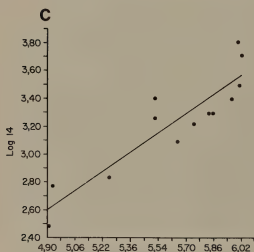
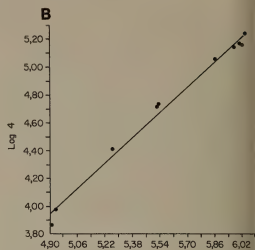
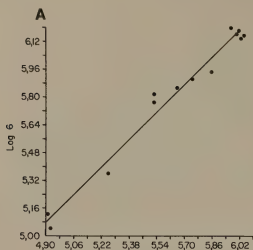
The basal cranial length of those fossils in the present series for which this parameter could be recorded ranged from 135 mm (BPI.FN. 904) to 410 mm (BPI.FN. 806). This range, if basal cranial length is accepted as an indicator of the general size of the cranium, can be accommodated comfortably within the ontogenetic size range for skulls of modern large reptiles (e.g. *Alligator* and *Crocodylus*). And, as mentioned previously, specimens of *Aulacephalodon* have been recovered from localities within a rather limited horizontal and vertical range. *Aulacephalodon* appears therefore to satisfy the requirements for a possible growth series as established by Olson & Miller (1951).

Coefficients of allometry and other relevant data for bivariate plots against basal cranial length are presented in Table 3. Selected bivariate plots of cranial measurements against basal cranial length are shown in Figure 2.

In no instance could linearity be rejected, by analysis of the t statistic, in favour of a possible parabolic (quadratic) relationship (Table 3). Correlation between variable sets is rather high; most correlation coefficients are greater than 0.95 (Table 3). The high correlation coefficients and the degree of clustering of the points about the slope lines suggest that the specimens studied here represent a morphologically homogeneous group of animals in various stages of ontogenetic development. This series includes the types of *Aulacephalodon haughtoni*, *A. latissimus*, *A. luckhoffi*, *A. pricei*, and *A. vanderhorsti*.

In several cases the allometric coefficients indicate isometric or nearly isometric growth relative to basal cranial length (e.g. variables 2, 3, 6, 8, 16, 21, 26), but in each instance the confidence intervals for β range from well below to well above isometry. Dodson (1975a) has noted that for *Alligator mississippiensis* coefficients as close to isometry as 0.98 or 1.02 can be shown to differ from 1.00 at $p = 0.02$ or even $p = 0.001$, an indication of the high degree of correlation between variables, which is conditioned, in part, by the magnitude of the ontogenetic size range of specimens of *Alligator*.

In three instances—palatal length (4), greatest cranial width (19), and the greatest width between the nasal bosses (25) (Fig. 1)—positive allometric



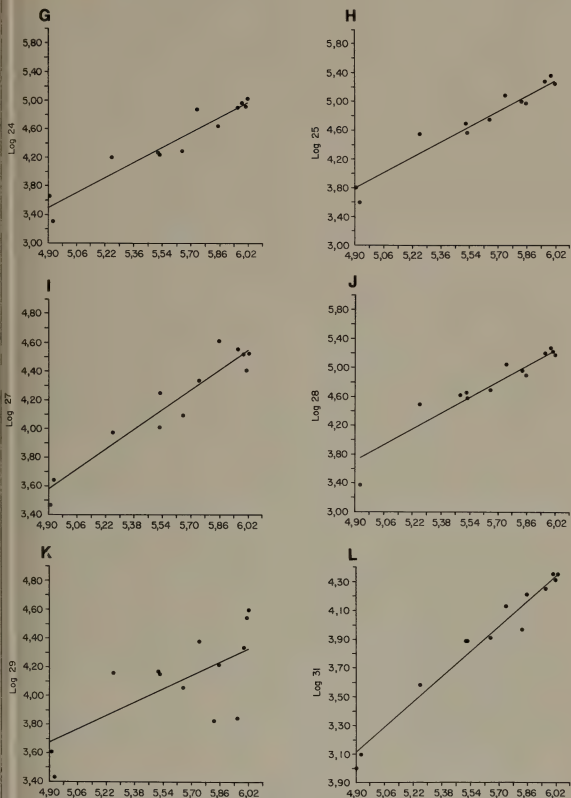


Fig. 2. A-L. Selected bivariate plots of *Aulacephalodon* crania. The scale on both axes is logarithmic. In each case the X-axis is basal skull length (variable 1). The solid line represents the calculated line of Bartlett's 'best fit'.

TABLE 3

Summary of data concerning relative growth and variability in *Aulacephalodon* (X = basal cranial length).

Y	N	β	α	β -CI	α -CI	r	df	t	RL
2	13	0.99	-0.46	0.87; 1.11	-0.50; -0.43	0.99	10	-0.713	No
3	13	0.99	-0.84	0.79; 1.19	-0.90; -0.78	0.97	10	0.444	No
4	10	1.15	-1.69	1.04; 1.26	-1.72; -1.65	1.00	7	-1.833	No
5	10	0.82	-0.52	0.63; 1.23	-0.62; -0.42	0.94	7	-1.036	No
6	12	1.00	0.18	0.85; 1.14	0.13; 0.22	0.99	9	0.069	No
7	12	0.91	0.19	0.63; 1.16	0.11; 0.28	0.95	9	-0.554	No
8	12	1.01	-0.78	0.59; 1.29	-0.89; -0.67	0.95	9	0.093	No
9	12	1.10	-2.64	0.78; 1.44	-2.74; -2.53	0.95	9	0.132	No
10	5	1.20	-1.49	—; 1.66	-1.80; -1.17	0.98	2	0.424	No
11	13	1.17	-2.13	0.86; 1.51	-2.23; -2.03	0.95	10	-0.886	No
12	11	1.12	-1.35	0.87; 1.53	-1.43; -1.26	0.96	8	-1.253	No
13	12	0.94	-0.67	0.59; 1.16	-0.76; -0.59	0.96	9	-1.192	No
14	13	0.87	-1.67	0.54; 1.17	-1.76; -1.57	0.91	10	1.756	No
15	10	0.81	-0.80	0.60; 1.01	-0.87; -0.73	0.97	7	-0.748	No
16	12	1.05	-2.95	0.64; 1.37	-3.07; -2.83	0.94	9	-0.470	No
17	12	0.91	-0.05	0.43; 1.39	-0.11; 0.20	0.86	9	0.063	No
18	11	1.14	-0.89	0.91; 1.45	-0.98; -0.81	0.96	8	2.070	No
19	11	1.21	-1.01	1.04; 1.33	-1.06; -0.96	0.99	8	0.754	No
20	10	0.89	-1.33	0.32; 1.13	-1.42; -1.24	0.96	7	-1.507	No
21	10	0.98	-0.91	0.71; 1.23	0.97; -0.84	0.98	7	-0.558	No
22	13	1.26	-2.60	0.80; 1.90	-2.77; -2.43	0.86	10	0.998	No
23	13	0.84	0.49	0.58; 1.04	0.42; 0.56	0.96	10	-1.205	No
24	12	1.31	-2.94	0.95; 1.64	-3.05; -2.83	0.96	9	0.580	No
25	13	1.33	-2.73	1.02; 1.57	-2.82; -2.65	0.97	10	0.669	No
26	13	1.01	-1.70	0.56; 1.34	-1.82; -1.59	0.93	10	0.163	No
27	12	0.87	-0.69	0.64; 1.10	-0.76; -0.61	0.96	9	-1.483	No
28	12	1.39	-3.08	0.81; 1.76	-3.20; -2.96	0.95	9	0.097	No
29	13	0.59	0.80	0.01; 1.07	0.63; 0.96	0.72	10	0.363	No
30	11	0.86	-0.76	0.31; 1.21	-0.91; -0.62	0.90	8	0.613	No
31	13	1.11	-2.33	0.91; 1.27	-2.39; -2.28	0.98	10	-0.139	No

Y = variable number; N = number of specimens; α -CI = 95% confidence interval for α ; β -CI = 95% confidence interval for β ; r = correlation coefficient; d.f. = degrees of freedom; t = Bartlett's test statistic; RL = rejection of linearity in favour of a parabolic relationship.

growth was indicated. On the other hand, whilst some eleven variables showed values of β less than 1.00, in all of these cases the 95 per cent confidence intervals ranged above isometry; variable 29, intertemporal width, showed the lowest value (0.59) but even here the upper end of the confidence limit ranged above isometry to 1.07. This parameter shows a particularly high degree of variability in terms of the magnitude of its allometric confidence limits and its low correlation coefficient (Table 3).

It is interesting to note that the diameters of both the tusks (variable 14) and the caniniform processes (variable 15) show negative allometric growth (Table 3), although the upper limits of the confidence intervals for each range to above isometry. It appears that the eruption, or replacement of the tusks, by which increasingly larger teeth were introduced, did not keep pace with cranial enlargement. Also, the size of the orbits, as judged by their length (variable 27), enlarged in a negative allometric manner compared to basal

cranial length (Table 3). This is generally characteristic of higher vertebrates, where the eyes are disproportionately large in young individuals.

Gould (1968) has noted that increase in size subjects organisms to different orders of forces and, thus, new morphological configurations to cope with these new forces are required. In his discussion of the allomorphy of species, Hennig (1966) maintained that knowledge of allometric correlation is important, because it permits recognition of linkages between different series of transformations that might otherwise not be recognized. New shapes produced by continuation of an ontogenetic allometric relationship into new size ranges are not independent taxonomic criteria (Gould 1966).

For the most part, the features which have been used variously in the diagnosis of new *aulacephalodont* species have been (i) the size of the nasal bosses, (ii) the shapes and sutural relationships of the individual bones of the cranium and (iii) the length-breadth ratio of the cranium.

Although several *Aulacephalodon* specimens have been described as possible 'juveniles' (Haughton 1917; Broom 1921), no description of a new species has taken into consideration the phenomenon of allometry. Cluver (1971), in a detailed study of another anomodont, *Lystrosaurus*, has recorded that minor changes in skull morphology, such as a change in the sutural relationships of bones, may be attributed to the size and consequently the ontogenetic age of individual specimens. Keyser (1972) has postulated that the characters which have been used to distinguish the various species of *Aulacephalodon* depend greatly upon the size of the individual.

It is evident that in *Aulacephalodon* rather marked changes in the shape of the cranium and its various parts occurred with increasing size. In general, the relative width of the skull across the zygomatic arches and across the prefrontal and nasal bosses, as well as the robusticity and sculpture of the temporal arches and other parts, show a rather dramatic increase with ontogenetic age (Fig. 3).

The results of the present investigation indicate that at least five of the type specimens of *Aulacephalodon* species could be interpreted as constituting a homogeneous ontogenetic growth series. Two other types—*A. hartzembergi* and *A. brodei*—have been examined also, and whilst these specimens were not subjected to allometric analysis, it is evident that they, too, form part of the same growth series. Although not every type and available specimen has been studied, the results of this preliminary investigation appear to support the contention that perhaps all the specimens, which have been regarded previously as belonging to different *Aulacephalodon* species, constitute a taxonomically homogeneous ontogenetic growth series of but a single species, *Aulacephalodon baini* (Owen).

SEXUAL DIMORPHISM

Sexual differences of both living and fossil reptiles are generally poorly expressed in the skeleton, and, as such, they are difficult to identify (Olson

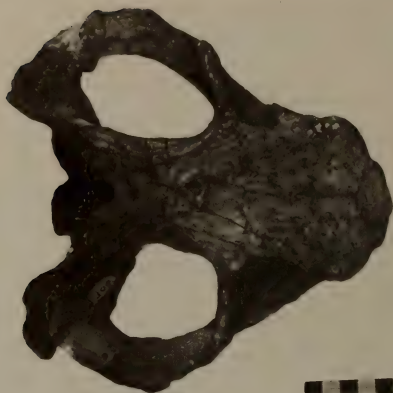
**B****A**



Fig. 3. Suggested ontogenetic series of *Aulacephalodon* crania. A. Small specimen, no. 4, BPLFN. 1207; basal cranial length 138 mm. B. Specimen no. 6, BPLFN. 300; basal cranial length 192 mm. C. Very large specimen, no. 5, BPLFN. 806 (holotype of *A. pricei*); basal cranial length 410 mm. Scales in cm.

1969). Dodson (1976) has used successfully two complementary approaches to define quantitatively sexual dimorphism in skulls of a small ceratopsian dinosaur. His first approach made use of bivariate allometric plots, a use of ratios, whilst the second was based on multivariate statistical analysis.

In the present study an attempt was made to assess quantitatively sexual dimorphism in a growth series of *Aulacephalodon* crania. Dodson's (1976) bivariate technique was utilized but application of the multivariate approach was not attempted owing to the small sample size of relatively complete crania. Bivariate plots of all thirty-one parameters were examined. For each case, individual values that lay above the line of Bartlett's 'best fit' were assigned a score of -1 , those below the line a score of $+1$, and values on the line were accorded a score of 0. Scores of 0 were very infrequent and were treated as indeterminate; thus they were not included in the final total of a score. The lower limit for the acceptance of either 'maleness' or 'femaleness' was set arbitrarily at 75 per cent, that is, at least three-quarters of the plotted points for an individual specimen lay to one side of the line. Only those specimens for which at least fifteen of the thirty possible variable plots were recorded were included in this part of the study (Table 4). Those fossils which fell above the line for 75 per cent of characters were considered to be male, whilst those that lay below the line for 75 per cent of traits were deemed to be female (see Dodson 1976).

Bivariate analysis of sexual dimorphism revealed that no single specimen exhibited a consistently male or female pattern. Two specimens, however, were consistent in expression in at least 74 per cent of the traits (specimens 2, SAM-8747, and 3, SAM-K1221), whilst a third (specimen 12, BPI.FN. 634) was consistent in 72 per cent of the characters. Accordingly, two of the specimens (2 and 12) may be accorded male status, whilst specimen 3 could be considered to be a female. Two of the fossils were completely indeterminate (7 and 8) and the others were only vaguely consistent in expression. In this analysis all available characters were considered; no selection of sexually distinctive features of the cranium was made. Thus, the technique utilized here differed from Dodson's (1976) in that he selected characters which were believed to be dimorphic for *Protoceratops*. It is possible that, in the bivariate analysis of sexual dimorphism in *Aulacephalodon*, those features which are related to sexual dimorphism could have been 'swamped' by a larger number of variables which are not dimorphic. Furthermore, as not all the specimens possessed all possible measurable features, it is possible that those traits which may be sexually related were not present in some of the fossils.

The principal cranial feature of *Aulacephalodon* which has been postulated to show sexual dimorphism is the relative size of the nasal bosses. Broom (1937) noted considerable variation in the size of the nasal bosses. He considered that the larger bosses were shown by male skulls, whilst females evinced more weakly developed bosses. He compared briefly two skulls which he considered represented a male and a female, and concluded also that the 'canine' tusks in

TABLE 4

 Bivariate sexual dimorphism scores for *Aulacephalodon* crania.
 Specimen

Variable no.	2	3	4	5	6	7	8	9	12	13	15	18
2	+	—	+	+	+	—	+	—	0	+	—	0
3	—	0	—	—	—	+	—	—	—	—	+	+
4			+	—	—	+	—	+	—	—	+	+
5			—	+	+	—	—	+	—	+	—	+
6	+	—	+	+	+	—	—	—	—	+	+	—
7	—	—	+	+	+	—	—	+	—	+	—	—
8	—	+	+	—	—	—	+	—	—	+	—	+
9	—		—	+	—	—	+	—	+	+	+	—
10			+	—	—		+			+		
11	+	+	+	—	—	—	—	+	+	—	—	+
12	—	—	—	+	+		+	—	+	+	+	—
13	—	+	+	+		+	+	+	—	—	—	—
14	+	+	—	—	+	+	—	+	—	+	—	+
15	—	+	+	—	+	—	+		—	+		—
16	—	+	+	+	—	+	0	+	0	+	—	+
17	—	+	—	—	+	+	+	—	—	+	—	+
18	+	+	—	0	+	—	—	—	—	—	—	—
19	—		+	+	—	—	+	—	—	+	—	—
20	—	—	+	+	—			—		—	+	+
21	—		—	+	+		+	—	+	—	+	—
22	+	+	—	—	—	—	—	+	+	+	—	—
23	—	—	+	+	+	+	+	—	—	—	+	—
24	—	+	+	—	—	—	+	—	+	+	—	+
25	—	+	+	+	—	0	+	—	—	+	—	+
26	—	+	+	+	—	+	+	—	—	+	—	+
27	—	+	—	+	—	+	—	—	+	—	+	+
28	—	+	+	+	—		—	—	—	+	—	0
29	—	+	+	—	—	+	—	+	—	+	—	—
30	+	+	0	—	—	+	—	+	—	—	—	+
31	—	+	+	0	—	+	—	+	—	—	—	+
Dominant sign	—	+	+	+	—			—	—	+	—	+
Score	74	74	65	59	63	50	50	59	72	63	68	58

Score = percentage frequency of occurrence of the dominant sign. + = individual plot below the line of Bartlett's 'best fit'; — = individual plot above the line of Bartlett's 'best fit'; 0 = individual plot on the line. See text for explanation.

males are longer and further apart than in females. In his description of *A. cadlei* he noted the nasal bosses of the type to be smaller than those in the type of *A. rubidgei*, and he postulated that the former specimen was a female whilst the latter was a male (Broom 1948). The question of sexual dimorphism in dicynodont crania has been considered by several workers (Owen 1860, 1876; Broom 1912, 1932; Barry 1957; Tripathi & Satangi 1963). Cluver (1971) discussed the possibility that *Lystrosaurus* crania exhibited pronounced sexual dimorphism, but he concluded that the dimorphic skulls of that genus probably represent two groups of species. Keyser (1969) recorded that the nasal bosses of *Aulacephalodon* appear to increase in prominence concomitantly with an increase in skull size; he maintained also that the bosses were related to sexual dimorphism.

In light of the previous speculations which have related nasal boss size and shape variation to sexual dimorphism, these structures were examined both metrically and osteoscopically in the present series of crania.

As an indication of the relative size of the nasal bosses the length of the protuberances (variable 31), as well as the greatest width between them (variable 25), were considered. When these two parameters are compared to basal cranial length (Table 3), both are found to increase in a positive allometric fashion, although the confidence interval for nasal boss length ranges to below isometry. When these variables are considered against basal snout length (variable 3), the positive allometric nature of their growth rates is slightly more pronounced (Table 5) and the 95 per cent confidence limit for nasal boss length ranges as low as isometry only. The considerable degree of morphological variability which is evinced by the nasal bosses may be related to their rates of growth. Dodson (1975a, 1975b) found that in two living reptiles (*Alligator* and

TABLE 5

Summary of data concerning relative growth and variability in *Aulacephalodon* (X = basal snout length).

Y	N	β	α	β -CI	α -CI	r	df	t	RL
1	13	1,01	0,85	0,84; 1,27	0,79; 0,91	0,97	10	-0,444	No
2	13	1,00	0,38	0,73; 1,41	0,25; 0,48	0,93	10	-0,550	No
4	10	1,16	-0,71	1,09; 1,26	-0,74; -0,68	1,00	7	-0,912	No
5	10	0,83	0,18	0,60; 1,35	0,06; 0,30	0,93	7	-0,599	No
6	13	0,93	1,39	0,73; 1,16	1,32; 1,46	0,97	10	-0,548	No
7	13	0,93	0,93	0,67; 1,28	0,83; 1,03	0,93	10	0,480	No
8	14	1,01	0,07	0,69; 1,34	-0,04; 0,18	0,93	11	-0,113	No
9	12	1,11	-1,71	0,69; 1,77	-1,87; -1,54	0,88	9	-0,140	No
10	6	0,85	1,07	0,70; 2,18	0,61; 1,52	0,83	3	-0,747	No
11	15	1,13	-0,88	0,84; 1,51	-0,99; -0,77	0,92	12	-1,418	No
12	12	1,07	-0,13	0,81; 1,47	-0,22; -0,05	0,93	9	-2,404	Yes
13	13	0,99	-0,07	0,75; 1,22	-0,14; 0,01	0,97	10	0,353	No
14	15	0,88	-0,95	0,63; 1,16	-1,03; -0,86	0,92	12	1,186	No
15	10	0,80	-0,03	0,56; 1,09	-0,12; 0,06	0,95	7	-0,352	No
16	13	1,01	-1,88	0,70; 1,31	-1,98; -1,78	0,95	10	-0,220	No
17	13	0,86	1,09	0,43; 1,26	0,95; 1,22	0,88	10	-0,264	No
18	12	1,08	0,38	0,85; 1,42	0,29; 0,48	0,96	9	1,344	No
19	12	1,12	0,46	0,85; 1,42	0,36; 0,55	0,97	9	-0,082	No
20	10	0,92	-0,67	0,35; 1,18	-0,77; -0,58	0,95	7	-1,849	No
21	11	1,03	-0,32	0,86; 1,41	-0,39; -0,25	0,96	8	-2,142	No
22	13	1,27	-1,53	0,77; 2,09	-1,72; -1,34	0,83	10	0,687	No
23	15	0,82	1,32	0,60; 1,05	1,25; 1,40	0,94	12	-1,572	No
24	14	1,24	-1,45	0,94; 1,57	-1,56; -1,35	0,95	11	0,910	No
25	15	1,51	-2,44	1,02; 2,13	-2,63; -2,26	0,89	12	-0,705	No
26	15	0,97	-0,58	0,59; 1,34	0,70; -0,45	0,89	12	-0,114	No
27	14	0,89	-0,03	0,75; 1,06	-0,08; 0,03	0,97	11	-1,449	No
28	13	1,20	-0,98	0,44; 1,69	-1,13; -0,82	0,90	10	-0,076	No
29	15	0,68	0,86	0,25; 1,06	0,73; 1,00	0,80	12	-0,078	No
30	13	1,12	-1,36	0,75; 1,60	-1,46; -1,16	0,90	10	0,651	No
31	15	1,17	-1,62	1,00; 1,37	-1,69; -1,56	0,98	12	-1,507	No

Y = variable number; N = number of specimens; α -CI = 95% confidence interval for α ; β -CI = 95% confidence interval for β ; r = correlation coefficient; d.f. = degrees of freedom; t = Bartlett's test statistic; RL = rejection of linearity in favour of a parabolic relationship.

Sceloporus) the greatest variability is associated with the most strongly allometric variables. In *Aulacephalodon* the greatest width between the bosses (which includes the breadth of both these structures as well as the rest of the nasal bones) shows the strongest allometric growth compared to basal snout length (Table 5). The allometric nature of these protuberances is not quite so marked when basal skull length is used for comparison, but in the latter case (Table 3) fewer specimens were included. The width across the nasal bosses shows both stronger allometric growth and more variability than the length of these structures when the two are compared to either basal cranial (Table 3) or basal snout (Table 5) lengths.

Three rather distinct types of nasal boss morphology, as assessed qualitatively, were discerned in the present cranial series (Figs 4–5). In crania with 'Type 1' boss development (Figs 4A, 5A), the lateral margins of the nasal bones above the external nasal apertures show very little, if any, form of swelling; when viewed from above, the dorsal surface of the snout tapers anteriorly from the orbits. Nasal bosses of the second type (Figs 4B, 5B) project laterally to various degrees from the edges of the nasals above the external nares. The bosses project laterally and form a nearly flat (horizontal) surface with the nasal bones. Bosses of 'Type 3' (Figs 4C, 5C) also project laterally above the external nasal apertures, but are more swollen in appearance than those of the second type; they project dorsally as well as laterally. The third type of nasal protuberance projects above the dorsal surface of the nasal bones, and in several specimens a longitudinal 'gutter' is present between the midline of the nasal bones and the boss on each side.

The first type of nasal boss was found in small crania, whilst the second and third types appear in larger skulls. Nasal bosses of 'Type 1' are very slightly developed (Fig. 6). The second and third types of nasal bosses appear to increase in size with cranial length, but the two types can be distinguished in nearly all cases throughout a broadly overlapping range of individual size (Fig. 6).

In the present sample, skulls which show 'Type 3' nasal bosses achieve a larger size than those with bosses of 'Type 2' morphology. This apparent size difference, however, may be an artefact of sampling. Several specimens (e.g. 19, 25–29) show a nasal boss configuration that appears to be intermediate between the second and third types. Although the morphological configuration of the nasal bosses may be altered through burial deformation (e.g. a 'Type 3' could be changed to a 'Type 2' through vertical diagenetic pressures), in the vast majority of cases these structures seem to have suffered very little from such deformation. In one specimen (15, BPI.FN. 2983) the nasal bosses had been pushed ventrally so that they form a nearly horizontal transverse plane with the nasal bones, but the bilateral shallow longitudinal troughs are still discernible owing to the presence of the median sagittal nasal ridge.

Inasmuch as the present sample of *Aulacephalodon* crania exhibits a rather high degree of biometric homogeneity, it seems reasonable to suggest that the morphological differences shown by the nasal bosses may be sexual in nature.

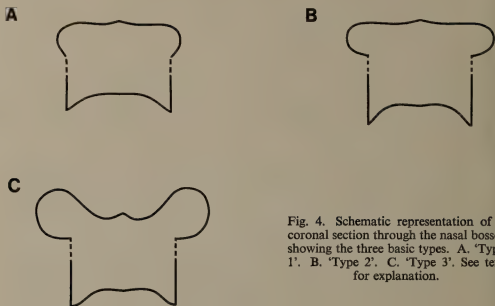


Fig. 4. Schematic representation of a coronal section through the nasal bosses showing the three basic types. A. 'Type 1'. B. 'Type 2'. C. 'Type 3'. See text for explanation.

Various cranial sizes, or inferred ontogenetic stages, are present for both the second and third types of nasal bosses, whilst the smallest, and presumably youngest, skulls in the present sample evince a 'Type 1' nasal boss. It is possible that the nasal bosses in *Aulacephalodon* could have served as a sexually selective feature for mate recognition and/or agonistic display mechanisms, or for both. Furthermore, the several relatively large crania (specimens 19, 25-26 and 29) which show nasal bosses intermediate in form between 'Types 2 and 3' may represent the antimodal overlap of the bimodal distribution of a discontinuous feature such as sexual dimorphism. However, a number of the crania in which the nasal bosses are indeterminate are broken and poorly preserved.

It is possible that those crania with the more robust, 'Type 3' nasal bosses represent the male condition. The same has been postulated obliquely by previous workers (Broom 1937, 1948; Keyser 1969).

In the present series, it appears that, once a certain cranial size had been reached, the nasal bosses assumed one of two rather distinct configurations (Fig. 7). It is suggested that the smaller crania, in which the nasal bosses are only slightly expressed ('Type 1'), represent relatively young, sexually immature individuals. Specimen 6 (BPI.FN. 300) possesses rather small nasal bosses of the 'Type 2' (female) configuration (Fig. 8). This fossil has been identified tentatively as female (Figs 6-7). It is possible that with growth the nasal bosses of both sexes were of a 'Type 2' configuration before sexual maturity (or dimorphism) had been achieved; the smallest positively identifiable male cranium is somewhat larger than the specimen in question. If this sample is at all representative of *Aulacephalodon*, then it seems that the expression of

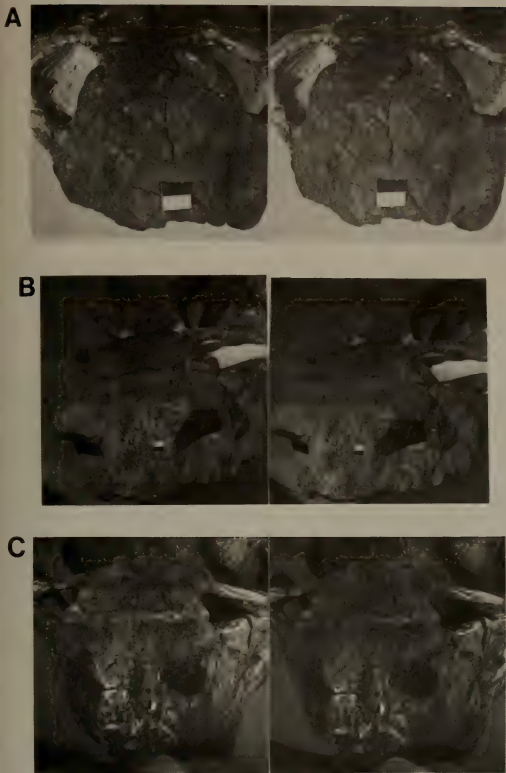


Fig. 5. Stereophotos of the three basic nasal boss configurations. A. 'Type 1', specimen no. 7, BPI.FN. 904. B. 'Type 2', specimen no. 18, BPI.FN. 304. C. 'Type 3', specimen no. 17, BPI.FN. 493. See text for explanation. Scales in cm.

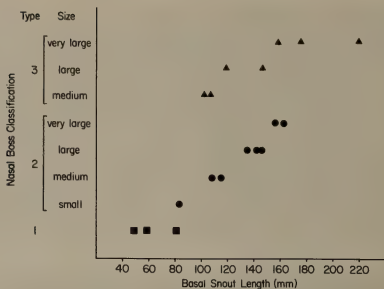


Fig. 6. Relationship of nasal boss size and morphotype to cranial (snout length) size.

sexual dimorphism was achieved by individuals when snout length was between about 80 and 95 mm and basal cranial length approximately 190 to 245 mm.

The nasal bosses enlarged in a positive allometric manner compared to snout and cranial lengths, but it appears that the general morphology of these structures remained relatively constant with an increase in individual size.

Another feature of the cranium also appears to be related to sexual dimorphism. In large presumptive male crania (e.g. specimens 5, 13, 15 and 17), the lateral border of the zygomatic arch shows a thickening of the squamosal. This body thickening is in the form of a gently curved, ventrally directed convexity, the lateral margin of which shows a rugose texture (Fig. 9). Large female crania, on the other hand, show no such thickening of the zygomatic arch; in these specimens the lateral margin of the squamosal is thinner and the arch has parallel dorsal and ventral surfaces. In smaller male crania the zygomatic arch is similar to those of females in that there is no sign of squamosal thickening. The significance of this thickening of the anterior portion of the zygomatic arch in larger male crania is enigmatic. Keyser (1969) noted that these squamosal 'bosses' may have been related to the jaw adductor musculature; but if this were the case it is puzzling why only the older males developed these structures.

Of the three crania sexed by bivariate analysis, the metrical diagnosis of two of them (specimens 3 and 12) agreed with the non-metrical assignment; however, whilst the third skull (specimen 2) was male according to the bivariate sexing technique, it shows a 'Type 2' nasal boss configuration, and although it is a fairly large specimen the zygomatic arches are not thickened.

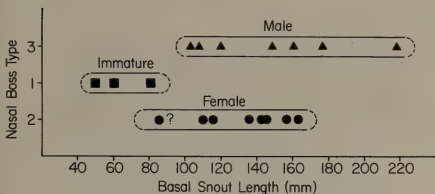


Fig. 7. Graphic representation of nasal boss morphotype compared to cranial (snout length) size. The questionable individual is specimen no. 6, BPI.FN. 300 (see Figs 3B, 8).

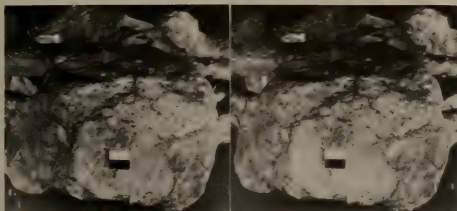


Fig. 8. Stereoview of nasal boss size and morphology of specimen no. 6, BPI.FN. 300. Scale in cm.

DISTRIBUTION

An important factor to be considered in an analysis of the biological implications of the Type 1, 2 and 3 nasal boss configurations of *Aulacephalodon* is the geographic and temporal distribution of these various types. The geographical distribution of the localities which have yielded the crania examined in this study is shown in Figure 10. Although the Madumabisa Mudstone 'Formation' is situated a considerable distance from the concentration of lower Beaufort localities in the Cape Province, the *Aulacephalodon* specimens found at the Zambian sites do not appear to be morphologically distinct from those recovered from the *Cistecephalus* and lower *Daptocephalus* zone sediments of South Africa (Drysdall & Kitching 1963).

The specimens examined in this study were recovered from localities over a rather limited geographical (Fig. 10) as well as vertical (Keyser 1969; Kitching

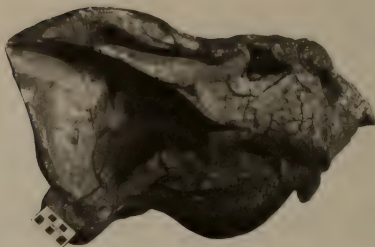


Fig. 9. Lateral view of a large *Aulacephalodon* skull showing the thickening of the squamosal at the anterior end of the zygomatic arch. Specimen no. 17, BPI.FN. 493. Scale in cm.

1977) range. There is no horizontal separation by either size or nasal boss morphology of the specimens; furthermore, two specimens (4 and 17) from the same site (Fig. 10R, Table 6) show considerable difference in both size and nasal boss configuration. One (BPI.FN. 1207) is a small individual with only minimal nasal boss development, whilst the other specimen (BPI.FN. 493) represents the largest skull in the sample and it possesses well-developed 'Type 3' nasal protuberances. Specimens which show variously Type 2 and 3 nasal bosses have been recovered from at least one other locality (Fig. 10I, Table 6).

The facts that specimens of various sizes with different nasal boss configurations have been recovered from single localities, and that there is no geographic or stratigraphic separation of specimens evincing different sizes and shapes, appear to support the hypothesis that the *Aulacephalodon* specimens studied here do, indeed, represent an ontogenetic growth series of a single species which evinced sexual dimorphism.

DISCUSSION

During the deposition of the *Cistecephalus* Zone sediments the terrain appears to have been characterized by broad, low gradient floodplains traversed by numerous, intermittent streams (Keyser 1970). The climate throughout this time, as inferred from the abundance of calcareous concretions and of 'desert roses', composed of pseudomorphs of calcite after gypsum (Keyser 1966), may have been sufficiently dry to warrant the term arid. The flora of the lower Beaufort seems to lack variety, the most commonly occurring plants being the equisetaleans, *Schizoneura* and *Phyllothea* (Keyser 1970). Both Keyser (1969, 1970) and Kitching (1977) have commented on the improbability

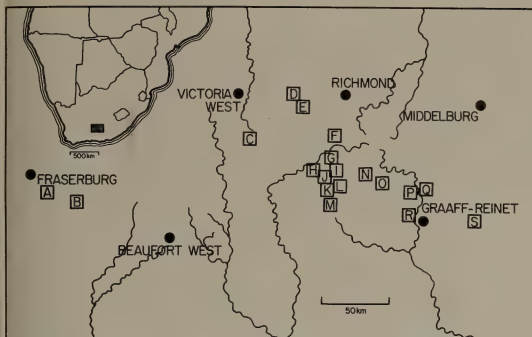


Fig. 10. Distribution of the localities from which the specimens examined in this study were recovered. A. Murraysburg commonage. B. Swaelkrans. C. Leeufontein. H. Ringsfontein. I. Graaff-Reinet commonage. J. Katbosch. K. Vleiplaats. L. Bultfontein. M. Leeuriviersberg. N. Houd Constant. O. Roodebloem. P. Matjiesfontein. Q. Petersburg. R. Hoekplaas. S. Ferndale.

of the synchronous and apparently sympatric coexistence of a large number of anomodont species under the ecological conditions envisaged for *Cistecephalus* Zone times. Keyser has noted the possibility that only a single species of *Aulacephalodon*, a large dicynodont, is represented in these strata.

Biometric (allometric) analysis of a fairly large sample of *Aulacephalodon* crania, which included seven of the seventeen type specimens, indicates that at least this group of crania constitutes a homogeneous and probably species-specific, ontogenetic growth series.

The ecological roles of at least two large extant reptiles, *Alligator* and *Crocodylus*, have been observed to change continuously throughout the life of the animal (Cott 1961; Dodson 1975a), the size and type of food obtained being a function of the size of the individual. Analogous food changes probably occurred with the Triassic cynodont *Diademodon* (Grine *et al.* 1978). Similar changes in the ecological role of *Aulacephalodon baini* might have taken place as a function of ontogenetically increasing body size, and thus increased the breadth of the niche occupied by this reptile; but this is by no means certain. Keyser (1972) has pointed out that *Aulacephalodon* possessed a relatively short, broad snout, reinforced by anterior longitudinal palatal ridges, and he concluded that biting was restricted to the tips of the jaws. *Aulacephalodon* probably had a horny beak at the tip of the snout, and it is possible that the changes in the

TABLE 6

Tabulation of locality data. The code corresponds to the legend for Figure 10.

Code	Locality	Specimen	Nasal boss morphotype	Sex
A	Murraysburg commonage	7	1	indet.
B	Swaelkrans	5	3	male
C	Leeurivierspoort	33	3	male
D	Modderfontein	9	2	female
E	Bloukop	8	2	female
F	Oudeplaas	13	3	male
G	Leeufontein	12	3	male
H	Ringsfontein	11	3	male
I	Graaff-Reinet commonage	15	3	male
		10	3	male
		18	2	female
		21	2	female
J	Katbosch	6	2	? female
K	Vleiplaats	3	2	female
L	Bultfontein	14	2	female
M	Leeuriviersberg	32	3	male
N	Houd Constant	20	2	female
		31	2	female
O	Roodebloem	1	1	indet.
P	Matjiesfontein	16	2	female
Q	Petersburg	19	? 3	? male
R	Hoeksplaas	4	1	indet.
		17	3	male
S	Ferndale	2	2	female

shape of the snout that occurred during growth may have been further accentuated by the beak.

Although sexual differences of both extant and fossil reptiles are generally poorly expressed in the skeleton, Dodson (1976) has provided convincing evidence of sexual dimorphism in skulls of the late Cretaceous dinosaur, *Protoceratops andrewsi*. He showed sexual dimorphism to be an important source of variability in this ceratopsian, and found that it was reflected in many characters of the skull apart from the obvious ones.

A preliminary and limited biometric (bivariate) analysis of *Aulacephalodon* skulls indicated that only three of the specimens in the sample could be assigned even possibly to a sex: two specimens were provisionally accorded male status whilst a third was regarded as possibly female. The nasal bosses of *Aulacephalodon* have been regarded by several workers as being related possibly to sexual dimorphism e.g. Broom 1937, 1948; Keyser 1969). A simple size and shape analysis of these structures throughout an ontogenetic growth series has revealed that they do, indeed, appear to be related to sexual differences (Figs 6-7).

The smallest crania exhibit only slightly developed nasal bosses ('Type 1'), whilst larger skulls evince either a somewhat flattened, laterally projecting boss ('Type 2') or a more bulbous, expanded structure ('Type 3'). The sex of the smaller crania could not be determined although Houghton (1917) considered SAM-3328 (specimen 1, described by Broom in 1921 as the type of *Bainia*

haughtoni) to be a 'young male'. It was not possible in this study to refute or substantiate Haughton's claim.

Those crania which showed a 'Type 2' nasal boss are believed to represent females, whilst it is suggested that males evinced a more strongly developed ('Type 3') protuberance. Although the bivariate sexing technique used here proved to be generally inconclusive, as discussed above, three specimens showed relatively consistent biplot patterns (SAM-8747, BPI.FN. 634—males; SAM-K1221—female). The qualitative determination of sex, based solely upon nasal boss configuration, agreed with the biometric determination in two instances; but in the case of SAM-8747, a relatively large specimen, whilst the biparametric technique indicated 'maleness', it was deemed to be a female on the shape of its nasal bosses.

It is suggested that males possessed relatively more strongly developed bosses than females, and that these structures might have served some sexual selective function. They might have served as important visual signs in a mate recognition system and/or as agonistic display mechanisms. Keyser (1969) has suggested that the bosses could have protected the eyes (from thorny vegetation or during fighting), supported horny growths, and possibly even served a thermoregulatory function.

While the size of the nasal bosses is related in an allometrically positive fashion to the growth of the cranium (as represented by either basal snout or basal cranial lengths), the morphotypic expression of their general configuration appears to have been established at the attainment of sexual dimorphism and to have remained recognizably distinct throughout continued ontogenetic development. Thus, the male and female configurations are discernible over a rather large size range, whilst the smaller specimens show only minimal boss development. If nasal boss morphology is sexually related, as indeed it appears to be, and if the present sample is representative of *Aulacephalodon*, then it seems that sexual dimorphism was first expressed when the base of the cranium attained a length of between 190 and 245 mm.

The locality data appear to support the hypothesis that the present sample represents a morphometrically homogeneous, ontogenetic growth series of a single species of *Aulacephalodon* and that with age this species exhibited sexual dimorphism of the nasal bosses and of the anterior portion of the temporal arch. The confirmation or refutation of these hypotheses must, however, await a more detailed biometrical and osteoscopic analysis of a larger series of specimens which includes all the type specimens of *Aulacephalodon*.

SUMMARY AND CONCLUSIONS

A biometrical (allometric) analysis of a number of *Aulacephalodon* crania was undertaken. The sample included representatives of various supposed species as well as the holotypes of a number of these. The results of this investigation indicate that this sample represents a morphometrically homogeneous,

species specific, ontogenetic growth series. The features utilized previously as taxonomic criteria can be understood as one result of allometric growth.

A qualitative analysis indicates that nasal boss morphology is related to sexual dimorphism. It is apparent that the smallest (ontogenetically youngest) individuals showed no or minimal nasal boss development, and that sexual maturity or at least the earliest expression of sexual dimorphism may have occurred in individuals with a basal cranial length of between 190 and 245 mm. The larger male crania show a thickening of the lateral margin of the temporal arches, and this is not present in small male or any female skulls. Large male crania show a thickening of the anterior portion of the temporal arches.

The locality data for the specimens in this sample support the inference that this group of fossils represents a species-specific ontogenetic growth series, and that sexual dimorphism was expressed in the cranium of *Aulacophalodon baini*.

ACKNOWLEDGEMENTS

The fossil material was made available to us through the generous offices of the Bernard Price Institute for Palaeontological Research, Johannesburg, the Geological Survey, Pretoria, the South African Museum, Cape Town, and the Transvaal Museum, Pretoria. Discussions with Drs M. A. Cluver, J. W. Kitching, and A. W. Keyser, who helped in the mapping of the locality data, were beneficial to this paper. We thank Dr M. A. Cluver, and Professors J. A. Hopson, M. Raath, and P. V. Tobias for reading and constructively criticizing this paper. We thank Miss J. Groom for drawing the text figures and Mr H. Thackway for photography. This work was supported in part by a grant to F. E. Grine by the University of the Witwatersrand Senate Research Committee.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14-15A

Nucula (Leda) *bicuspidata* Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a-b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nicklès, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8-9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

S. M. TOLLMAN F. E. GRINE
&
B. D. HAHN

ONTOGENY AND SEXUAL DIMORPHISM IN
AULACEPHALODON (REPTILIA,
ANOMODONTIA)

VOLUME 81 PART 5

APRIL 1980

ISSN 0303-2515

507.68

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- (a) *Centred masthead to consist of*
 Title: informative but concise, without abbreviations and not including the names of new genera or species
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 Number of illustrations (figures, enumerated maps and tables, in this order)
- (b) *Abstract of not more than 200 words, intelligible to the reader without reference to the text*
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- (d) *Introduction*
- (e) *Subject-matter of the paper, divided into sections to correspond with those given in table of contents*
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- (h) *References*
- (i) *Abbreviations, where these are numerous*

3. MANUSCRIPT, to be submitted in triplicate, should be typewritten and neat, double spaced with 2.5 cm margins all round. First lines of paragraphs should be indented. Tables and a list of legends for illustrations should be typed separately, their positions indicated in the text. All pages should be numbered consecutively.

Major headings of the paper are centred capitals; first subheadings are shouldered small capitals; second subheadings are shouldered italics; third subheadings are indented, shouldered italics. Further subdivisions should be avoided, as also enumeration (never roman numerals) of headings and abbreviations.

Footnotes should be avoided unless they are short and essential.

Only generic and specific names should be underlined to indicate italics; all other marking up should be left to editor and publisher.

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- 'Smith (1969: 36, fig. 16) describes . . .'
- 'As described (Smith 1969a, 1969b; Jones 1971)'
- 'As described (Haughton & Broom 1927) . . .'
- 'As described (Haughton *et al.* 1927) . . .'

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(b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc. to the year for more than one paper by the same author in that year, e.g. Smith (1969*a*, 1969*b*) and not Smith (1969, 1969*a*).

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Examples (note capitalization and punctuation)

- BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
- FISCHER, P.-H. 1948. Données sur la résistance et de la vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.
- FISCHER, P.-H., DUVAL, M. & RAFFY, A. 1933. Études sur les échanges respiratoires des littorines. *Archs Zool. exp. gén.* 74: 627-634.
- KOHN, A. J. 1960*a*. Ecological notes on *Conus* (Mollusca: Gastropoda) in the Trincomalee region of Ceylon. *Ann. Mag. nat. Hist.* (13) 2: 309-320.
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- THIELE, J. 1910. Mollusca: B. Polyplacophora, Gastropoda marina, Bivalvia. In: SCHULTZE, L. *Zoologische und anthropologische Ergebnisse einer Forschungsreise im westlichen und zentralen Süd-Afrika* 4: 269-270. Jena: Jena. *Denkschr. med.-naturw. Ges. Jena* 16: 269-270.

(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume 81 Band
April 1980 April
Part 5 Deel



THE SOUTH AFRICAN MUSEUM'S
MEIRING NAUDE CRUISES
PART 10
STATION DATA 1977, 1978, 1979

Compiled by
ELIZABETH LOUW

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

are issued in parts at irregular intervals as material
becomes available

Obtainable from the South African Museum, P.O. Box 61, Cape Town

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na gelang van die
beskikbaarheid van stof

Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad

OUT OF PRINT/UIT DRUK

1, 2(1-3, 5-8), 3(1-2, 4-5, 8, t.-p.i.), 5(1-3, 5, 7-9),
6(1, t.-p.i.), 7(1-4), 8, 9(1-2, 7), 10(1-3),
11(1-2, 5, 7, t.-p.i.), 15(4-5), 24(2), 27, 31(1-3), 32(5), 33

Copyright enquiries to the South African Museum

Kopieregnavrae aan die Suid-Afrikaanse Museum

ISBN 0 908407 90 4

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

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(With 1 figure and 6 tables)

[MS. accepted 6 December 1979]

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INTRODUCTION

In 1975 the South African Museum's Department of Marine Biology embarked on the first of a series of cruises in deeper waters (about 500 m and more) off the east coast of southern Africa. Station data for the 1975 and 1976 cruises have been published (Louw 1977). During the period 1977-9 three additional cruises were carried out in areas south of the region sampled in 1975 and 1976. Publications dealing with collections from the 1977, 1978 and 1979 cruises will in most instances give station numbers only, and refer to the present paper for further data.

THE CRUISES

Grants from the South African National Council for Oceanographic Research (SANCOR) and assistance from the South African Museum enabled the Department of Marine Biology to undertake the three cruises aboard the R.V. *Meiring Naude*. From 9 to 18 May 1977 work was carried out south of Durban, Natal, in the area 30°01'S to 31°30'S and 30°03'E to 32°02'E with bottom depths ranging from 690 m to 2 600 m. In 1978 the area from 32°40'S to 34°11'S and 28°50'E to 27°08'E was worked during the period 24 May to 1 June, in depths ranging from 80 m to 2 880 m. In 1979 permission was obtained to fish off the coast of the Republic of Transkei and from 18 to 28 June the area 30°46'S to 32°37'S and 30°39'E to 28°54'E was sampled in depths of 82 m to 2 820 m. In both 1978 and 1979 some stations that were worked were in relatively shallow water due to adverse weather and sea conditions which prevented

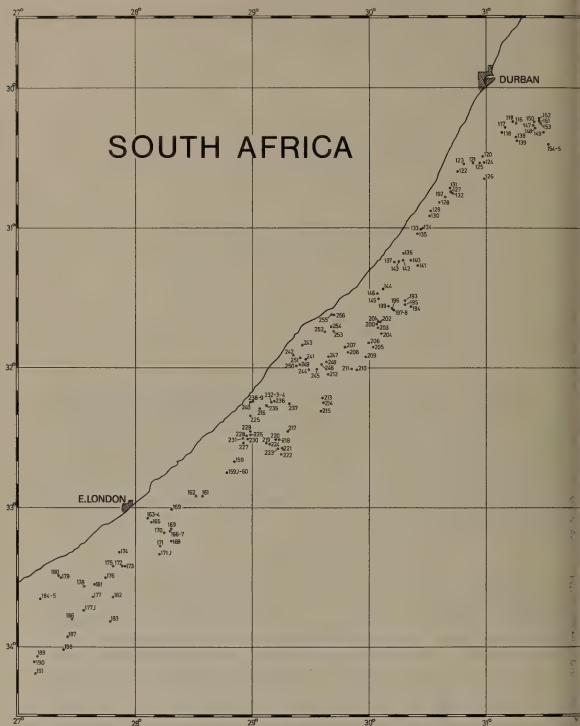


Fig. 1. Chart of the area sampled during the 1977 (stations SM 116-158), 1978 (stations SM 159-191), and 1979 (stations SM 192-256) cruises of the South African Museum on the R.V. Meiring Naude.

sampling further off shore. In all 141 stations were occupied during the three cruises and station data are presented in Tables 1, 3 and 5. Relevant temperature data are provided in Tables 2, 4 and 6.

The gear used was basically the same as for the 1975 and 1976 cruises, but with the following changes:

Use of the IOSN and IKMT was discontinued

The small square-framed neuston net (Neuston_s) used in 1976 was replaced during the 1977 cruise with a larger oval-framed net with floats (Neuston_L)

In addition to the RMT with uniform anchovy mesh (RMT_M), a similar net with stepped-mesh (RMT_S) was used at some mid-water stations

A double beam trawl (Menzies 1964: 103, fig. 14; Belyaev 1966: 18, fig. 17) replaced the 18 ft beam trawl on the 1979 cruise

The material collected is housed in the South African Museum collections, with duplicate fish material in the J. L. B. Smith Institute of Ichthyology, Grahamstown, and duplicate decapod and isopod Crustacea in the U.S. National Museum of Natural History, Washington, D.C. Some animal groups are still available for study by interested biologists. These include Gasteropoda, Pelecypoda, Brachiopoda, Anthozoa, Mysidacea, Tanaidacea and Euphausiacea.

NOTES FOR TABLES

S, D and N following SM numbers, e.g. SM 124S, SM 124D and SM 124N, indicate shallow Bongo, deep Bongo and Neuston net hauls respectively, at the same station.

J following SM numbers, e.g. SM 159J, indicates surface fishing with jiggers or dip-nets at night lights after completion of the haul at the station of the same number.

The beam trawl was lost at SM 137 (during the third cruise), at SM 165 (during the fourth cruise) and the double beam trawl was lost at SM 256 (at the end of the fifth cruise).

Bathythermograph column in Tables 1, 3 and 5 indicates the number (BT-) of the bathythermograph profile to which one should refer for temperature data relevant to that station, and for which temperatures at selected depths are given in Tables 2, 4 and 6, respectively.

In Table 1

** SM 115 Neuston net was towed during the RMT haul

* SM 126 An Expendable Bathythermograph (XBT) was used instead of a standard bathythermograph

† SM 119 RMT_M was on the bottom for part of the haul

In Tables 4, 6

* Temperatures at 0m were obtained from the readings on the Multipoint chart for sea surface temperature.

In Table 6

** There are no temperature readings for BT-50 and BT-51 due to equipment failure.

TABLE I
Station data for the third cruise, 9-18 May 1977.

Station No.	Position		Time		Date	Bottom Depth	Fishing Depth		Gear	Bathy-thermograph No.	Sea surface temp.	Ship's speed
	Latitude	Longitude	Start	Fishing End			m	m			°C	
	°S	°E				m	m					knots
SM 116	30°15,0'	31°15,4'	1347	1407-1447	1516	820	820		Heavy dredge		25,99	0
SM 117	30°17,5'	31°10,0'	1553	1620-1650	1725	820	820		Beam trawl		26,00	1,84
SM 118S	30°18,9'	31°08,1'		1746-1752					Bongo	BT-1	26,00	1,39
SM 118D	30°18,9'	31°08,1'		1758-1821					Bongo	BT-1	25,98	1,83
SM 119	30°14,4'	31°13,9'	1943	2104-2134	2152	750	750		RMTM	BT-1	25,65	1,68
SM 120S	30°29,7'	30°58,0'		0617-0624					Bongo	BT-2	25,90	0,33
SM 120D	30°29,7'	30°58,0'		0631-0651					Bongo	BT-2	25,87	1,71
SM 121	30°32,2'	30°52,8'	0830	0931-1040	1130	900-625	900-625		Beam trawl		25,93	1,86
SM 122S	30°36,0'	30°45,0'		1334-1340					Bongo	BT-3	26,17	1,89
SM 122D	30°36,0'	30°45,0'		1346-1408					Bongo	BT-3	26,15	1,78
SM 123	30°33,4'	30°48,6'	1507	1525-1555		690	690		Heavy dredge		26,14	0
SM 124S	30°32,5'	30°59,2'		1805-1811					Bongo	BT-4	26,22	1,44

SM 126	30°39,6'	30°59,6'	2217	2250-2350	0115	10.5.77	1820	464-0	RMTM	BT-6*	26,15	3,73
SM 127S	30°44,7'	30°41,6'		0601-0607		11.5.77		50	Bongo	BT-7	25,61	1,46
SM 127D	30°44,7'	30°41,6'		0611-0632		11.5.77		150	Bongo	BT-7	25,62	1,78
SM 127N	30°44,7'	30°41,6'		10 min.		11.5.77		0	Neustons	—	25,62	1,78
SM 128	30°49,1'	30°35,7'	0740	0813-0849	0929	11.5.77	830-930	830-930	Beam trawl		25,80	0
SM 129	30°53,4'	30°31,7'	0942	1012-1115		11.5.77	850	850	Heavy dredge		25,78	0
SM 130S	30°55,2'	30°30,8'		1239-1245		11.5.77		50	Bongo	BT-8	25,78	1,88
SM 130D	30°55,2'	30°30,8'		1248-1309		11.5.77		212	Bongo	BT-8	25,84	1,90
SM 130N	30°55,2'	30°30,8'		10 min		11.5.77		0	NeustonL	—	25,84	1,90
SM 131	30°43,2'	30°40,8'	1545	1610-1642	1715	11.5.77	780	780	Beam trawl		26,03	0
SM 132	30°45,4'	30°42,2'	2002	2048-2149	2239	11.5.77	1750	830-0	RMTM	BT-9	26,11	3,65
SM 133S	31°01,2'	30°26,5'		0606-0612		12.5.77		50	Bongo	BT-10	25,51	1,34
SM 133D	31°01,2'	30°26,5'		0618-0640		12.5.77		212	Bongo	BT-10	25,59	1,49
SM 133N	31°01,2'	30°26,5'		5 min		12.5.77		0	NeustonL	—	25,59	1,49
SM 134	31°00,0'	30°27,2'	0859	0930-1030	1110	12.5.77	900	900	Beam trawl		25,40	0
SM 135S	31°03,4'	30°24,2'		1214-1220		12.5.77		50	Bongo	BT-11	25,64	1,60
SM 135D	31°03,4'	30°24,2'		1229-1251		12.5.77		212	Bongo	BT-11	25,63	1,63
SM 136S	31°11,0'	30°17,1'		0602-0608		13.5.77		50	Bongo	BT-12	25,32	1,63
SM 136D	31°11,0'	30°17,1'		0614-0635		13.5.77		212	Bongo	BT-12	25,28	1,60

TABLE 1
Station data for the third cruise, 9–18 May 1977.

Station No.	Position		Time			Date	Bottom Depth	Fishing Depth	Gear	Bathy-thermograph No.	Sea surface temp.	Ship's speed
	Latitude	Longitude	Start	Fishing	End							
	°S	°E					m	m			°C	knots
SM 116	30°15,0'	31°15,4'	1347	1407–1447	1516	9.5.77	820	820	Heavy dredge		25,99	0
SM 117	30°17,5'	31°10,0'	1553	1620–1650	1725	9.5.77	820	820	Beam trawl		26,00	1,84
SM 118S	30°18,9'	31°08,1'		1746–1752		9.5.77		50	Bongo	BT-1	26,00	1,39
SM 118D	30°18,9'	31°08,1'		1758–1821		9.5.77		212	Bongo	BT-1	25,98	1,83
SM 119	30°14,4'	31°13,9'	1943	2104–2134	2152	9.5.77	750	750	RMT _M	BT-1	25,65	1,68
SM 120S	30°29,7'	30°58,0'		0617–0624		10.5.77		59	Bongo	BT-2	25,90	0,33
SM 120D	30°29,7'	30°58,0'		0631–0651		10.5.77		212	Bongo	BT-2	25,87	1,71
SM 121	30°32,2'	30°52,8'	0830	0931–1040	1130	10.5.77	900–625	900–625	Beam trawl		25,93	1,86
SM 122S	30°36,0'	30°45,0'		1334–1340		10.5.77		50	Bongo	BT-3	26,17	1,89
SM 122D	30°36,0'	30°45,0'		1346–1408		10.5.77		212	Bongo	BT-3	26,15	1,78
SM 123	30°33,4'	30°48,6'	1507	1525–1555		10.5.77	690	690	Heavy dredge		26,14	0
SM 124S	30°32,5'	30°59,2'		1805–1811		10.5.77		50	Bongo	BT-4	26,22	1,44
SM 124D	30°32,5'	30°59,2'		1817–1838		10.5.77		212	Bongo	BT-4	26,21	1,91
SM 124N	30°32,5'	30°59,2'		10 min.		10.5.77		0	Neustons		26,21	1,91
SM 125	30°32,2'	30°57,5'	1909	1929–2029	2050	10.5.77	1280	415–0	RMT _M	BT-5	26,18	1,71
SM 126	30°39,6'	30°59,6'	2217	2250–2350	0115	10.5.77	1820	464–0	RMT _M	BT-6*	26,15	3,73
SM 127S	30°44,7'	30°41,6'		0601–0607		11.5.77		50	Bongo	BT-7	25,61	1,46
SM 127D	30°44,7'	30°41,6'		0611–0632		11.5.77		150	Bongo	BT-7	25,62	1,78
SM 127N	30°44,7'	30°41,6'		10 min.		11.5.77		0	Neustons	—	25,62	1,78
SM 128	30°49,1'	30°35,7'	0740	0813–0849	0929	11.5.77	830–930	830–930	Beam trawl		25,80	0
SM 129	30°53,4'	30°31,7'	0942	1012–1115		11.5.77	850	850	Heavy dredge		25,78	0
SM 130S	30°55,2'	30°30,8'		1239–1245		11.5.77		50	Bongo	BT-8	25,78	1,88
SM 130D	30°55,2'	30°30,8'		1248–1309		11.5.77		212	Bongo	BT-8	25,84	1,90
SM 130N	30°55,2'	30°30,8'		10 min		11.5.77		0	Neustons _L	—	25,84	1,90
SM 131	30°43,2'	30°40,8'	1545	1610–1642	1715	11.5.77	780	780	Beam trawl		26,03	0
SM 132	30°45,4'	30°42,2'	2002	2048–2149	2239	11.5.77	1750	830–0	RMT _M	BT-9	26,11	3,65
SM 133S	31°01,2'	30°26,5'		0606–0612		12.5.77		50	Bongo	BT-10	25,51	1,34
SM 133D	31°01,2'	30°26,5'		0618–0640		12.5.77		212	Bongo	BT-10	25,59	1,49
SM 133N	31°01,2'	30°26,5'		5 min		12.5.77		0	Neustons _L	—	25,59	1,49
SM 134	31°00,0'	30°27,2'	0859	0930–1030	1110	12.5.77	900	900	Beam trawl		25,40	0
SM 135S	31°03,4'	30°24,2'		1214–1220		12.5.77		50	Bongo	BT-11	25,64	1,60
SM 135D	31°03,4'	30°24,2'		1229–1251		12.5.77		212	Bongo	BT-11	25,63	1,63
SM 136S	31°11,0'	30°17,1'		0602–0608		13.5.77		50	Bongo	BT-12	25,32	1,63
SM 136D	31°11,0'	30°17,1'		0614–0635		13.5.77		212	Bongo	BT-12	25,28	1,60

TABLE 1 (continued)

Station No.	Position		Time		Date	Bottom Depth	Fishing Depth	Gear	Bathy-thermograph No.	Sea surface temp.	Ship's speed
	Latitude	Longitude	Start	Fishing End							
	°S	°E				m	m			°C	knots
SM 137	31°15,3'	31°12,6'	0805	0837-	13.5.77	870	—	Beam trawl		—	—
SM 138	30°21,3'	30°15,7'	1915	1959-2102	2148	1320	830-0	RMT _M	BT-13	23,82	3,26
SM 139	30°22,8'	31°16,2'	2304	2320-0021	0045	1400	250-0	RMT _M	BT-13	24,42	3,24
SM 140	31°14,4'	30°20,9'	0915	1009-1109	1209	1560	1120-0	RMT _M	BT-14	26,03	3,17
SM 141S	31°16,6'	30°24,3'		1243-1249			50	Bongo	BT-15	26,03	1,49
SM 141D	31°16,6'	30°24,3'		1254-1315			212	Bongo	BT-15	26,06	1,42
SM 142	31°14,0'	30°16,9'	1415	1452-1522	1605	1400	1400	Heavy dredge		25,69	0
SM 143S	31°14,7'	30°14,7'		1806-1812			50	Bongo	BT-16	25,83	1,62
SM 143D	31°14,7'	30°14,7'		1816-1840			212	Bongo	BT-16	25,81	1,61
SM 144S	31°26,1'	30°06,5'		0604-0610			50	Bongo	BT-17	26,00	1,36
SM 144D	31°26,1'	30°06,5'		0614-0635			212	Bongo	BT-17	26,00	1,61
SM 145	31°30,4'	30°04,0'	0735	0825-0925	1034	2000	1129-0	RMT _M	BT-17	25,94	3,05
SM 146S	31°28,6'	30°03,9'		1209-1214			50	Bongo	BT-18	26,00	1,59

SM 147N	30°16,0'	31°24,5'		10 min	17.5.77	—	0	Neuston _L	—	23,86	1,34
SM 148	30°17,1'	31°25,2'	0710	0756–0856	17.5.77	1800	750–0	RMT _M	BT-20	24,25	3,31
SM 149S	30°19,4'	31°29,3'		1205–1211	17.5.77		50	Bongo	BT-21	24,20	1,60
SM 149D	30°19,4'	31°29,3'		1215–1237	17.5.77		212	Bongo	BT-21	24,25	1,62
SM 149N	30°19,4'	31°29,3'		10 min	17.5.77		0	Neuston _L	—	24,25	1,62
SM 150	30°14,7'	31°25,4'	1410	1437–1552	1620	17.5.77	1000	Heavy dredge		23,70	0
SM 151	30°14,0'	31°27,6'	1630	1652–1715	1737	17.5.77	900	Biol. dredge		23,82	0
SM 152S	30°13,5'	31°27,5'		1804–1810	17.5.77		50	Bongo	BT-22	23,80	1,62
SM 152D	30°13,5'	31°27,5'		1814–1834	17.5.77		212	Bongo	BT-22	23,80	1,75
SM 152N	30°13,5'	31°27,5'		10 min	17.5.77		0	Neuston _L	—	23,80	1,75
SM 153	30°15,5'	31°28,2'	1852	1932–2032	2123	17.5.77	664–0	RMT _M	BT-23	23,78	3,24
SM 154	30°24,5'	31°32,5'	2239	2308–0008	17.5.77	2600	500–0	RMT _M	BT-23	24,10	3,29
SM 155	30°24,5'	31°32,5'		10 min	17.5.77		0	**Neuston _L		24,10	3,29
SM 156S	30°01,5'	31°57,2'		0602–0609	18.5.77		50	Bongo	BT-24	25,95	1,39
SM 156D	30°01,5'	31°57,2'		0613–0634	18.5.77		212	Bongo	BT-24	25,92	1,64
SM 156N	30°01,5'	31°57,2'		10 min	18.5.77		0	Neuston _L	—	25,92	1,64
SM 157	30°05,5'	31°57,0'	0809	0849–0949	1040	18.5.77	750–0	RMT _M	BT-25	25,98	3,34
SM 158S	30°08,8'	32°02,0'		1209–1214	18.5.77		50	Bongo	BT-25	26,00	1,89
SM 158D	30°08,8'	32°02,0'		1218–1236	18.5.77		212	Bongo	BT-25	26,01	1,79

TABLE 1 (continued)

Station No.	Position		Time			Date	Bottom Depth	Fishing Depth	Gear	Bathy-thermo-graph No.	Sea surface temp.	Ship's speed
	Latitude	Longitude	Start	Fishing	End							
	°S	°E					m	m			°C	knots
SM 137	31°15,3'	31°12,6'	0805	0837-		13.5.77	870	—	Beam trawl		—	—
SM 138	30°21,3'	30°15,7'	1915	1959-2102	2148	14.5.77	1320	830-0	RMT _M	BT-13	23,82	3,26
SM 139	30°22,8'	31°16,2'	2304	2320-0021	0045	14.5.77	1400	250-0	RMT _M	BT-13	24,42	3,24
SM 140	31°14,4'	30°20,9'	0915	1009-1109	1209	15.5.77	1560	1120-0	RMT _M	BT-14	26,03	3,17
SM 141S	31°16,6'	30°24,3'		1243-1249		15.5.77		50	Bongo	BT-15	26,03	1,49
SM 141D	31°16,6'	30°24,3'		1254-1315		15.5.77		212	Bongo	BT-15	26,06	1,42
SM 142	31°14,0'	30°16,9'	1415	1452-1522	1605	15.5.77	1400	1400	Heavy dredge		25,69	0
SM 143S	31°14,7'	30°14,7'		1806-1812		15.5.77		50	Bongo	BT-16	25,83	1,62
SM 143D	31°14,7'	30°14,7'		1816-1840		15.5.77		212	Bongo	BT-16	25,81	1,61
SM 144S	31°26,1'	30°06,5'		0604-0610		16.5.77		50	Bongo	BT-17	26,00	1,36
SM 144D	31°26,1'	30°06,5'		0614-0635		16.5.77		212	Bongo	BT-17	26,00	1,61
SM 145	31°30,4'	30°04,0'	0735	0825-0925	1034	16.5.77	2000	1129-0	RMT _M	BT-17	25,94	3,05
SM 146S	31°28,6'	30°03,9'		1209-1214		16.5.77		50	Bongo	BT-18	26,00	1,59
SM 146D	31°28,6'	30°03,9'		1219-1239		16.5.77		212	Bongo	BT-18	25,99	1,49
SM 147S	30°16,0'	31°24,5'		0605-0611		17.5.77		50	Bongo	BT-19	24,86	1,34
SM 147D	30°16,0'	31°24,5'		0615-0635		17.5.77		212	Bongo	BT-19	23,86	1,34
SM 147N	30°16,0'	31°24,5'		10 min		17.5.77		0	Neuston _L	—	23,86	1,34
SM 148	30°17,1'	31°25,2'	0710	0756-0856		17.5.77	1800	750-0	RMT _M	BT-20	24,25	3,31
SM 149S	30°19,4'	31°29,3'		1205-1211		17.5.77		50	Bongo	BT-21	24,20	1,60
SM 149D	30°19,4'	31°29,3'		1215-1237		17.5.77		212	Bongo	BT-21	24,25	1,62
SM 149N	30°19,4'	31°29,3'		10 min		17.5.77		0	Neuston _L	—	24,25	1,62
SM 150	30°14,7'	31°25,4'	1410	1437-1552	1620	17.5.77	1000	1000	Heavy dredge		23,70	0
SM 151	30°14,0'	31°27,6'	1630	1652-1715	1737	17.5.77	900	900	Biol. dredge		23,82	0
SM 152S	30°13,5'	31°27,5'		1804-1810		17.5.77		50	Bongo	BT-22	23,80	1,62
SM 152D	30°13,5'	31°27,5'		1814-1834		17.5.77		212	Bongo	BT-22	23,80	1,75
SM 152N	30°13,5'	31°27,5'		10 min		17.5.77		0	Neuston _L	—	23,80	1,75
SM 153	30°15,5'	31°28,2'	1852	1932-2032	2123	17.5.77	1900	664-0	RMT _M	BT-23	23,78	3,24
SM 154	30°24,5'	31°32,5'	2239	2308-0008		17.5.77	2600	500-0	RMT _M	BT-23	24,10	3,29
SM 155	30°24,5'	31°32,5'		10 min		17.5.77		0	**Neuston _L		24,10	3,29
SM 156S	30°01,5'	31°57,2'		0602-0609		18.5.77		50	Bongo	BT-24	25,95	1,39
SM 156D	30°01,5'	31°57,2'		0613-0634		18.5.77		212	Bongo	BT-24	25,92	1,64
SM 156N	30°01,5'	31°57,2'		10 min		18.5.77		0	Neuston _L	—	25,92	1,64
SM 157	30°05,5'	31°57,0'	0809	0849-0949	1040	18.5.77	1300	750-0	RMT _M	BT-25	25,98	3,34
SM 158S	30°08,8'	32°02,0'		1209-1214		18.5.77		50	Bongo	BT-25	26,00	1,89
SM 158D	30°08,8'	32°02,0'		1218-1236		18.5.77		212	Bongo	BT-25	26,01	1,79

TABLE 2
Temperatures at selected depths as obtained from bathythermograph slides during the third cruise.

Depth	0 m	10 m	20 m	30 m	40 m	50 m	60 m	75 m	100 m	200 m	250 m	300 m	400 m	450 m
Bathythermo- graph No.	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C
BT-1	25,70	25,70	25,40	25,10	23,50	22,95	22,00	21,20	20,00	15,75	14,70	—	—	—
BT-2	25,85	25,80	25,80	25,80	25,80	25,80	24,00	23,00	21,80	16,90	15,70	—	—	—
BT-3	26,00	25,90	25,90	25,85	25,50	25,00	23,90	22,00	21,65	16,50	14,45	—	—	—
BT-4	26,00	26,00	26,00	26,00	26,00	26,00	24,00	22,70	21,05	15,90	15,00	—	—	—
BT-5	26,00	26,00	26,00	26,00	25,95	25,45	24,50	22,50	21,15	16,50	15,20	—	—	—
*BT-6	26,40	26,40	26,40	26,45	26,45	26,40	25,00	23,00	21,50	16,70	15,90	13,25	12,65	12,10
BT-7	25,50	25,50	25,50	25,45	25,20	24,15	22,75	22,00	20,80	15,65	13,10	—	—	—
BT-8	25,55	25,50	25,45	25,30	25,10	24,00	22,80	21,75	20,10	14,80	13,50	—	—	—
BT-9	26,00	26,00	26,00	26,00	26,00	26,00	24,95	22,50	20,35	16,40	15,00	—	—	—
BT-10	25,55	25,55	25,55	25,55	25,45	24,00	23,00	21,60	19,60	14,50	13,20	—	—	—
BT-11	25,70	25,70	25,70	25,65	24,75	24,05	23,15	21,00	17,60	14,40	—	—	—	—
BT-12	25,40	25,40	25,35	24,70	24,30	23,50	21,90	19,80	18,20	14,00	13,15	—	—	—
BT-13	23,80	23,70	23,50	22,80	20,15	19,10	18,00	16,90	15,50	13,60	12,50	—	—	—
BT-14	23,80	23,80	23,80	23,80	23,50	21,25	20,10	19,20	17,30	14,00	12,85	—	—	—
BT-15	26,10	26,10	26,10	26,10	26,10	26,10	24,00	22,40	20,20	15,10	14,00	—	—	—
BT-16	25,75	25,75	25,75	25,30	24,40	23,90	22,00	20,70	18,40	14,60	—	—	—	—
BT-17	26,00	26,00	26,00	26,00	26,00	26,00	23,70	22,50	20,05	15,00	14,00	—	—	—
BT-18	25,90	25,90	25,90	25,80	25,35	24,25	23,50	21,00	19,00	14,50	13,55	—	—	—
BT-19	24,00	23,90	23,80	22,45	21,10	20,05	19,00	17,75	16,45	13,65	12,50	—	—	—
BT-20	24,80	24,75	24,30	23,30	21,55	21,00	20,00	18,60	17,25	14,55	13,30	—	—	—
BT-21	24,10	24,00	24,75	22,40	20,80	20,00	19,20	17,90	16,50	13,70	12,90	—	—	—
BT-22	23,75	23,65	23,30	21,30	20,50	19,60	19,40	18,95	16,70	13,10	12,40	—	—	—
BT-23	23,55	23,55	23,50	23,35	23,00	21,75	20,30	18,65	17,20	14,00	12,90	—	—	—
BT-24	26,00	26,00	26,00	26,00	25,25	24,00	23,50	22,50	21,60	16,75	15,60	—	—	—
BT-25	25,90	25,90	25,90	25,90	25,70	25,00	24,55	23,80	21,20	16,70	14,95	—	—	—

Station data for the fourth cruise, 24 May-1 June 1978.

Station No.	Position		Start	Time		Date	Bottom Depth	Fishing Depth	Gear	Bathy-thermo-graph No.	Sea surface temp.	Ship's speed
	Latitude	Longitude		Fishing	End							
	°S	°E					m	m			°C	knots
SM 159	32°40,1'	28°30,8'	1932	1949-2049	2104	24.5.78	1000	690-0	RMTs	BT-26	23,41	2,90
SM 159J	32°45,6'	28°47,6'		2110-2155		24.5.78		0	JDNNL	—	23,68	0
SM 160	32°45,6'	28°47,6'	2156	2230-2338	2359	24.5.78	1140	583-0	RMTs	BT-26	23,81	4,34
SM 160N	32°45,6'	28°47,6'		2225-2243		24.5.78	1140	0	NeustonL		23,81	4,29
SM 161S	32°55,2'	28°34,8'		0625-0631		25.5.78		50	Bongo	BT-27	23,72	2,28
SM 161D	32°55,2'	28°34,8'		0640-0700		25.5.78		212	Bongo	BT-27	23,77	1,87
SM 162	32°55,0'	28°31,0'	0901	0921-0925	0952	25.5.78	630	630	Heavy Dredge		23,52	0,16
SM 163	33°04,6'	28°06,6'	0745	0750-0800		26.5.78	90	90	Heavy Dredge		23,15	0,29
SM 164	33°04,6'	28°06,6'	0813	0816-0840	0842	26.5.78	90	90	Heavy Dredge		22,96	0,28
SM 165	33°06,0'	20°08,3'	0907	0921-		26.5.78	—	—	Beam Trawl		—	—
SM 166S	33°10,0'	28°17,9'		0618-0623		27.5.78	1400	50	Bongo	BT-28	23,51	2,28
SM 166D	33°10,0'	28°17,9'		0629-0651		27.5.78	1400	212	Bongo	BT-28	23,57	2,13
SM 167	33°10,5'	28°17,5'	0921	0957-1100	1135	27.5.78	1450	1091-0	RMTs	BT-28	24,55	3,70
SM 168	33°14,2'	28°18,5'	1234	1259-1430	1459	27.5.78	1800	816-0	RMTs	BT-28	24,65	3,50
SM 169S	33°09,3'	28°18,6'		1742-1748		27.5.78	940	50	Bongo	BT-29	24,64	1,81
SM 169D	33°09,3'	28°18,6'		1753-1815		27.5.78	940	212	Bongo	BT-29	24,64	2,09

TABLE 3 (cont.)

Station No.	Position		Time		Date	Bottom Depth	Fishing Depth	Gear	Bartho-thermo-graph No.	Sea surface temp.	Ship's speed
	Latitude	Longitude	Start	Fishing End							
	°S	°E				m	m			°C	knots
SM 170	33°10,8'	28°14,8'	1922	1938-2039	2057	1580	708-0	RMT	BT-29	24,61	3,35
SM 170N ₁	33°10,8'	28°14,8'		1945-2001		1580	0	NeustonL	—	24,62	3,11
SM 170N ₂	33°10,8'	28°14,8'		2007-2027		1580	0	NeustonL	—	24,60	3,46
SM 171	33°16,4'	28°13,0'	2118	2143-2242	2310	2600	792-0	RMTs	BT-30	24,42	3,85
SM 171J	33°20,0'	28°12,7'		2315-2415		2600	0	JDNNL	—	24,52	0
SM 172D	33°25,1'	27°53,4'		0611-0633		1450	212	Bongo	BT-31	23,66	2,46
SM 172S	33°25,1'	27°53,4'		0640-0646		1450	50	Bongo	BT-31	23,84	2,18
SM 173	33°25,2'	27°54,7'	0937	1002-1106	1135	2020	683-0	RMTs	BT-31	24,17	3,92
SM 174	33°19,6'	27°52,4'	1353	1420-1440	1515	760	760	Heavy Dredge		23,36	0
SM 175S	33°25,3'	27°49,2'		1756-1802		720	50	Bongo	BT-32	23,12	2,43
SM 175D	33°25,3'	27°49,2'		1807-1831		760	212	Bongo	BT-32	23,10	2,25
SM 176	33°30,2'	27°45,5'	1933	1944-2044	2057	1300	308-0	RMTs	BT-32	23,18	3,03
SM 177	33°38,2'	27°38,3'	2138	2150-2250	2303	1140	400-0	RMTs	BT-32	23,61	0,23
SM 177J	33°44,5'	27°33,7'		± 2300			0	JDNNL	—	23,86	0,17



TABLE 3 (cont.)

Station No.	Position		Time			Date	Bottom Depth	Fishing Depth	Gear	Bathy-thermo-graph No.	Sea surface temp.	Ship's speed
	Latitude	Longitude	Start	Fishing	End							
	°S	°E					m	m			°C	knots
SM 170	33°10,8'	28°14,8'	1922	1938–2039	2057	27.5.78	1580	708–0	RMT	BT–29	24,61	3,35
SM 170N ₁	33°10,8'	28°14,8'		1945–2001		27.5.78	1580	0	Neuston _L	—	24,62	3,11
SM 170N ₂	33°10,8'	28°14,8'		2007–2027		27.5.78	1580	0	Neuston _L	—	24,60	3,46
SM 171	33°16,4'	28°13,0'	2118	2143–2242	2310	27.5.78	2600	792–0	RMT _S	BT–30	24,42	3,85
SM 171J	33°20,0'	28°12,7'		2315–2415		27.5.78	2600	0	JDN _{NL}	—	24,52	0
SM 172D	33°25,1'	27°53,4'		0611–0633		28.5.78	1450	212	Bongo	BT–31	23,66	2,46
SM 172S	33°25,1'	27°53,4'		0640–0646		28.5.78	1450	50	Bongo	BT–31	23,84	2,18
SM 173	33°25,2'	27°54,7'	0937	1002–1106	1135	28.5.78	2020	683–0	RMT _S	BT–31	24,17	3,92
SM 174	33°19,6'	27°52,4'	1353	1420–1440	1515	28.5.78	760	760	Heavy Dredge		23,36	0
SM 175S	33°25,3'	27°49,2'		1756–1802		28.5.78	720	50	Bongo	BT–32	23,12	2,43
SM 175D	33°25,3'	27°49,2'		1807–1831		28.5.78	760	212	Bongo	BT–32	23,10	2,25
SM 176	33°30,2'	27°45,5'	1933	1944–2044	2057	28.5.78	1300	308–0	RMT _S	BT–32	23,18	3,03
SM 177	33°38,2'	27°38,3'	2138	2150–2250	2303	28.5.78	1140	400–0	RMT _S	BT–32	23,61	0,23
SM 177J	33°44,5'	27°33,7'		±2300		28.5.78		0	JDN _{NL}	—	23,86	0,17
SM 178S	33°34,4'	27°34,2'		0753–0758		29.5.78	250	50	Bongo	BT–33	22,80	3,02
SM 178D	33°34,4'	27°34,2'		0804–0822		29.5.78	230	163	Bongo	BT–33	22,66	3,00
SM 179	33°30,3'	27°22,1'	1359	±27 min.	1430	29.5.78	80	80	Heavy Dredge		20,82	0,24
SM 180	33°29,4'	27°21,2'	1509	1511–1542	1544	29.5.78	80	80	Heavy Dredge		20,81	0,24
SM 181S	33°33,4'	27°39,6'		0607–0613		30.5.78		50	Bongo	BT–34	23,79	2,57
SM 181D	33°33,4'	27°39,6'		0618–0640		30.5.78		212	Bongo	BT–34	23,83	2,26
SM 182	33°38,2'	27°49,2'	0940	1028–1130	1219	30.5.78	2880	1517–0	RMT _S	BT–35	23,95	3,37
SM 183	33°48,8'	27°47,9'	1312	1338–1438	1509	30.5.78	2660	474–0	RMT _M	BT–35	24,21	3,60
SM 184	33°39,4'	27°11,7'	1001	1003–1034	1036	31.5.78	86	86	Heavy Dredge		20,49	0,43
SM 185	33°39,3'	27°11,6'	1042	1049–1155	1200	31.5.78	90	90	Heavy Dredge		20,47	0,33
SM 186	33°48,1'	27°27,4'	2024	2053–2153	2221	31.5.78	1720	583–0	RMT _S	BT–36	24,06	3,76
SM 187	33°55,9'	27°25,3'	2310	2351–0051	0132	31.5.78	2000	982–0	RMT _S	BT–36	23,69	3,48
SM 188S	34°01,5'	27°23,8'		0151–0156		1.6.78	1970	50	Bongo	BT–36	23,58	2,42
SM 188D	34°01,5'	27°23,8'		0202–0224		1.6.78	1970	212	Bongo	BT–36	23,59	2,36
SM 188N	34°01,5'	27°23,8'		0229–0246		1.6.78	1970	0	Neuston _L	—	23,68	5,24
SM 189S	34°04,3'	27°10,0'		0602–0608		1.6.78		50	Bongo	BT–37	23,91	2,44
SM 189D	34°04,3'	27°10,0'		0615–0640		1.6.78		212	Bongo	BT–37	23,91	2,30
SM 190	34°06,3'	27°08,3'	0904	0945–1044	1120	1.6.78	2000	658–0	RMT _S	BT–37	23,90	3,99
SM 191	34°11,5'	27°08,5'	1232	1308–1410	1451	1.6.78	2340	542–0	RMT _S	BT–37	23,52	3,78

TABLE 4
Temperatures at selected depths, as obtained from bathythermograph profiles during the fourth cruise.

Depth	*0 m	10 m	20 m	30 m	40 m	50 m	60 m	70 m	75 m	100 m	200 m	300 m	400 m	500 m	600 m	700 m	800 m	900 m	1 000 m
Bathy-thermo-graph No.	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C
BT-26	23.41	—	24.57	24.57	23.90	22.10	20.85	19.87	19.18	17.42	15.05	13.38	12.17	10.70	8.81	7.85	7.00	—	—
BT-27	23.77	—	24.08	24.08	21.75	20.70	19.50	19.43	18.88	16.90	14.35	12.75	11.92	10.57	8.62	7.62	6.08	5.02	4.12
BT-28	23.57	—	24.42	24.42	24.38	24.31	22.75	21.05	20.60	18.61	14.65	13.40	11.98	10.72	9.14	7.83	6.85	5.58	4.86
BT-29	24.64	24.78	24.79	24.65	24.55	24.05	23.05	22.00	21.72	18.82	14.06	12.60	11.32	10.20	8.28	7.15	5.93	5.12	—
BT-30	24.42	24.48	24.49	24.44	24.38	24.27	24.11	23.35	23.00	20.17	15.44	13.60	12.38	10.97	9.14	7.67	7.04	5.68	5.28
BT-31	23.66	—	23.92	23.79	23.42	21.96	21.35	20.17	19.41	16.90	12.70	10.78	8.86	7.42	6.98	—	—	—	—
BT-32	23.10	23.18	23.12	23.05	22.90	22.15	21.22	20.41	19.95	16.17	13.22	11.80	8.61	—	—	—	—	—	—
BT-33	22.66	—	22.83	22.80	21.28	20.50	18.95	16.81	16.40	14.87	12.91	—	—	—	—	—	—	—	—
BT-34	23.83	—	23.93	23.58	21.50	20.32	19.62	18.85	18.50	17.20	13.54	12.22	10.33	8.44	7.21	—	—	—	—
BT-35	23.95	23.95	23.98	23.98	23.89	22.19	21.27	20.53	20.21	18.74	15.52	13.97	12.59	11.20	10.03	9.10	6.90	6.67	5.62
BT-36	24.06	23.88	23.89	23.89	23.88	22.61	21.11	20.07	19.85	18.10	14.60	12.50	11.21	10.00	8.65	6.74	6.01	5.31	—
BT-37	23.91	—	24.18	24.18	24.18	22.82	21.70	20.35	19.71	18.22	14.60	12.50	11.15	10.00	8.13	6.36	6.01	5.89	5.13

TABLE 5
Station data for the fifth cruise, 18-28 June 1979.

Station No.	Position		Time		Date	Bottom Depth	Fishing Depth	Gear	Bathy-thermograph No.	Sea surface temp.	Ship's speed
	Latitude	Longitude	Start	Fishing End							
	°S	°E				m	m			°C	knots
SM 192	30°46,6'	30°39,1'	—	1815-2250	—	18.6.79	1200	0	JDNNL	—	21,62
SM 193S	31°30,8'	30°17,7'	—	0612-0616	—	19.6.79	—	53	Bongo	BT-38	22,36
SM 193D	31°30,8'	30°17,7'	—	0632-0654	—	19.6.79	—	212	Bongo	BT-38	22,38
SM 193N	31°30,8'	30°17,7'	—	0704-0714	—	19.6.79	—	0	NeustonL	—	22,39
SM 194	31°34,0'	30°20,6'	1045	1138-1239	1342	19.6.79	2800	2166-1150	RMTs	BT-39	22,59
SM 195	31°33,1'	30°18,2'	1447	1601-1701	1818	19.6.79	2740	1050-840	RMTs	BT-39	23,27
SM 196S	31°34,3'	30°11,5'	—	1900-1906	—	19.6.79	2280	53	Bongo	BT-40	23,03
SM 196D	31°34,3'	30°11,5'	—	1913-1940	—	19.6.79	2280	212	Bongo	BT-40	23,03
SM 196N	31°34,4'	30°11,5'	—	1957-2007	—	19.6.79	2280	0	NeustonL	—	23,00
SM 197	31°35,4'	30°11,8'	2105	2110-2207	2215	19.6.79	2300	150	RMTs	BT-40	22,97
SM 198	31°35,4'	30°11,8'	—	2133-2148	—	19.6.79	2300	0	NeustonL	—	22,96
SM 199	31°33,9'	30°08,8'	2318	2330-0031	0048	19.6.79	2130	250	RMTs	BT-41	22,92
SM 200S	31°41,8'	30°03,2'	—	0605-0609	—	20.6.79	2100	53	Bongo	BT-42	22,69
SM 200D	31°41,8'	30°03,2'	—	0618-0638	—	20.6.79	2100	212	Bongo	BT-42	22,70
SM 200N	31°41,8'	30°03,2'	—	0652-0702	—	20.6.79	2100	0	NeustonL	—	22,72
SM 201	31°40,2'	30°03,9'	0830	0858-0958	1103	20.6.79	2300	1333-1000	RMTs	BT-42	22,59
SM 202S	31°40,0'	30°04,7'	—	1212-1218	—	20.6.79	—	53	Bongo	BT-43	22,48
SM 202D	31°40,0'	30°04,7'	—	1223-1241	—	20.6.79	—	212	Bongo	BT-43	22,55
SM 203	31°42,9'	30°03,9'	1504	1538-1642	1810	20.6.79	2320	1750-1166	RMTs	BT-43	22,94

TABLE 5 (cont.)

Station No.	Position		Time		Date	Bottom Depth	Fishing Depth		Gear	Bathy-thermograph No.	Sea surface temp.	Ship's speed
	Latitude	Longitude	Start	Fishing End			m	m			°C	
		°S					m	m				knots
SM 204S	31°45,8'	30°04,7'	—	1921-1928	—	2580	53		Bongo	BT-44	23,17	2,02
SM 204D	31°45,8'	30°04,7'	—	1935-2000	—	2580	212		Bongo	BT-44	23,17	1,74
SM 204N	31°45,8'	30°04,7'	—	2012-2022	—	2580	0		NeustonL	—	23,32	3,21
SM 205	31°51,1'	30°01,7'	2123	2135-2238	2257	2680	585-500		RMTs	BT-44	23,28	4,06
SM 206	31°49,0'	29°59,0'	—	2315-0045	—	2600	0		JDNNL	—	23,17	0,00
SM 207S	31°51,6'	29°47,6'	—	0603-0610	—	2700	53		Bongo	BT-45	22,82	1,56
SM 207D	31°51,6'	29°47,6'	—	0617-0636	—	2700	212		Bongo	BT-45	22,82	1,40
SM 207N	31°51,6'	29°47,6'	—	0700-0705	—	2700	0		NeustonL	—	22,82	3,30
SM 208	31°53,8'	29°48,8'	0850	0935-1042	1151	2280	1320-870		RMTM	BT-45	22,90	3,85
SM 209	31°55,8'	29°57,1'	1522	1602-1710	1818	2820	1260-1050		RMTM	BT-46	23,25	3,50
SM 210S	32°01,3'	29°53,4'	—	1930-1936	—	2740	53		Bongo	BT-46	23,33	2,10
SM 210D	32°01,3'	29°53,4'	—	1943-2001	—	2740	212		Bongo	BT-46	23,33	1,85
SM 210N	32°01,3'	29°53,4'	—	2014-2021	—	2740	0		NeustonL	—	23,33	3,36
SM 211	32°00,8'	29°50,8'	2046	2101-2203	2223	2700	415		RMTM	BT-47	23,34	3,42
SM 212	32°03,4'	29°38,8'	—	0000-0100	—	2050	0		JDNNL	—	23,01	0,00
SM 213S	32°13,0'	29°34,9'	—	0605-0610	—	2300	53		Bongo	BT-48	22,74	—
SM 213D	32°13,0'	29°34,9'	—	0614-0634	—	2300	260		Bongo	BT-48	22,83	—
SM 214	32°15,1'	29°36,1'	0923	1003-1108	1205	2440	1390-1260		RMTs	BT-49	22,23	2,51
SM 215S	32°18,5'	29°35,1'	—	1322-1327	—	—	53		Bongo	BT-49	23,24	2,40
SM 215D	32°18,5'	29°35,1'	—	1333-1351	—	—	212		Bongo	BT-49	23,24	1,82

SM 217D	32°27,7'	29°18,0'	—	0610-0629	—	23.6.79	2250	212	Bongo	—	22,27	1,95
SM 217N	32°27,7'	29°18,0'	—	0641-0651	—	23.6.79	2250	0	NeustonL	—	22,36	3,05
SM 218	32°30,8'	29°13,4'	0906	0946-1049	1153	23.6.79	2200	916-875	RMT _M	—	22,66	3,22
SM 219S	32°32,3'	29°07,0'	—	1225-1230	—	23.6.79	—	60	Bongo	—	22,56	1,74
SM 219D	32°32,3'	29°07,0'	—	1235-1254	—	23.6.79	—	212	Bongo	—	22,56	2,05
SM 220	32°31,3'	29°11,9'	1400	1441-1558	1657	23.6.79	2170	1416-1250	RMT _M	BT-52	—	3,67
SM 221	32°34,2'	29°15,0'	1725	1758-1859	1945	23.6.79	2470	1170-840	RMT _M	BT-52	22,99	3,25
SM 222S	32°37,3'	29°14,7'	—	2039-2044	—	23.6.79	2470	43	Bongo	BT-52	23,03	1,83
SM 222D	32°37,3'	29°14,7'	—	2049-2110	—	23.6.79	2470	193	Bongo	BT-52	23,00	1,91
SM 222N	32°37,3'	29°14,7'	—	2117-2127	—	23.6.79	2470	0	NeustonL	—	23,08	2,15
SM 223	32°34,4'	29°13,1'	2133	2157-2301	2338	23.6.79	2380	670	RMT _M	BT-53	22,92	3,27
SM 224	32°33,4'	29°09,2'	0023	0044-0147	0216	24.6.79	2030	663-600	RMT _M	BT-53	22,90	3,59
SM 225S	32°20,4'	28°59,3'	—	0605-0611	—	24.6.79	—	38	Bongo	BT-54	22,10	1,95
SM 225D	32°20,4'	28°59,3'	—	0615-0636	—	24.6.79	—	212	Bongo	BT-54	22,15	1,81
SM 225N	32°20,4'	28°59,3'	—	0643-0653	—	24.6.79	—	0	NeustonL	—	22,12	2,58
SM 226	32°28,6'	28°58,8'	0855	0916-0947	1008	24.6.79	710-775	710-775	Heavy Dredge	BT-54	22,00	0,00
SM 227	32°32,1'	28°55,8'	1109	1141-1211	1243	24.6.79	775-790	775-790	Dbl. Beam Trawl	BT-55	21,99	0,67
SM 228	32°29,5'	28°57,1'	1518	1536-1609	1631	24.6.79	700-650	700-650	Heavy Dredge	BT-55	22,33	0,00
SM 229	32°27,8'	28°58,9'	1748	1806-1836	1900	24.6.79	670-740	670-740	Dbl. Beam Trawl	BT-56	22,59	0,00
SM 230S	32°30,6'	28°57,0'	—	1921-1928	—	24.6.79	630	38	Bongo	BT-56	22,58	1,73
SM 230D	32°30,6'	28°57,0'	—	1934-1956	—	24.6.79	630	172	Bongo	BT-56	22,64	1,88
SM 231	32°30,0'	28°54,8'	—	2015-2300	—	24.6.79	550	0	JDN _{NL}	—	22,63	0,00



TABLE 5 (cont.)

Station No.	Position		Time			Date	Bottom Depth	Fishing Depth	Gear	Bathy-thermograph No.	Sea surface temp.	Ship's speed
	Latitude	Longitude	Start	Fishing	End							
	°S	°E					m	m			°C	knots
SM 204S	31°45,8'	30°04,7'	—	1921–1928	—	20.6.79	2580	53	Bongo	BT-44	23,17	2,02
SM 204D	31°45,8'	30°04,7'	—	1935–2000	—	20.6.79	2580	212	Bongo	BT-44	23,17	1,74
SM 204N	31°45,8'	30°04,7'	—	2012–2022	—	20.6.79	2580	0	Neuston _L	—	23,32	3,21
SM 205	31°51,1'	30°01,7'	2123	2135–2238	2257	20.6.79	2680	585–500	RMT _S	BT-44	23,28	4,06
SM 206	31°49,0'	29°59,0'	—	2315–0045	—	20.6.79	2600	0	JDN _{NNL}	—	23,17	0,00
SM 207S	31°51,6'	29°47,6'	—	0603–0610	—	21.6.79	2700	53	Bongo	BT-45	22,82	1,56
SM 207D	31°51,6'	29°47,6'	—	0617–0636	—	21.6.79	2700	212	Bongo	BT-45	22,82	1,40
SM 207N	31°51,6'	29°47,6'	—	0700–0705	—	21.6.79	2700	0	Neuston _L	—	22,82	3,30
SM 208	31°53,8'	29°48,8'	0850	0935–1042	1151	21.6.79	2280	1320–870	RMT _M	BT-45	22,90	3,85
SM 209	31°55,8'	29°57,1'	1522	1602–1710	1818	21.6.79	2820	1260–1050	RMT _M	BT-46	23,25	3,50
SM 210S	32°01,3'	29°53,4'	—	1930–1936	—	21.6.79	2740	53	Bongo	BT-46	23,33	2,10
SM 210D	32°01,3'	29°53,4'	—	1943–2001	—	21.6.79	2740	212	Bongo	BT-46	23,33	1,85
SM 210N	32°01,3'	29°53,4'	—	2014–2021	—	21.6.79	2740	0	Neuston _L	—	23,33	3,36
SM 211	32°00,8'	29°50,8'	2046	2101–2203	2223	21.6.79	2700	415	RMT _M	BT-47	23,34	3,42
SM 212	32°03,4'	29°38,8'	—	0000–0100	—	22.6.79	2050	0	JDN _{NNL}	—	23,01	0,00
SM 213S	32°13,0'	29°34,9'	—	0605–0610	—	22.6.79	2300	53	Bongo	BT-48	22,74	—
SM 213D	32°13,0'	29°34,9'	—	0614–0634	—	22.6.79	2300	260	Bongo	BT-48	22,83	—
SM 214	32°15,1'	29°36,1'	0923	1003–1108	1205	22.6.79	2440	1390–1260	RMT _S	BT-49	22,23	2,51
SM 215S	32°18,5'	29°35,1'	—	1322–1327	—	22.6.79	—	53	Bongo	BT-49	23,24	2,40
SM 215D	32°18,5'	29°35,1'	—	1333–1351	—	22.6.79	—	212	Bongo	BT-49	23,24	1,82
SM 216	32°17,5'	29°04,4'	—	2200–0200	—	22.6.79	200	0	JDN _{NNL}	—	21,26	0,00
SM 217S	32°27,7'	29°18,0'	—	0559–0605	—	23.6.79	2250	53	Bongo	—	22,17	2,01
SM 217D	32°27,7'	29°18,0'	—	0610–0629	—	23.6.79	2250	212	Bongo	—	22,27	1,95
SM 217N	32°27,7'	29°18,0'	—	0641–0651	—	23.6.79	2250	0	Neuston _L	—	22,36	3,05
SM 218	32°30,8'	29°13,4'	0906	0946–1049	1153	23.6.79	2200	916–875	RMT _M	—	22,66	3,22
SM 219S	32°32,3'	29°07,0'	—	1225–1230	—	23.6.79	—	60	Bongo	—	22,56	1,74
SM 219D	32°32,3'	29°07,0'	—	1235–1254	—	23.6.79	—	212	Bongo	—	22,56	2,05
SM 220	32°31,3'	29°11,9'	1400	1441–1558	1657	23.6.79	2170	1416–1250	RMT _M	BT-52	—	3,67
SM 221	32°34,2'	29°15,0'	1725	1758–1859	1945	23.6.79	2470	1170–840	RMT _M	BT-52	22,99	3,25
SM 222S	32°37,3'	29°14,7'	—	2039–2044	—	23.6.79	2470	43	Bongo	BT-52	23,03	1,83
SM 222D	32°37,3'	29°14,7'	—	2049–2110	—	23.6.79	2470	193	Bongo	BT-52	23,00	1,91
SM 222N	32°37,3'	29°14,7'	—	2117–2127	—	23.6.79	2470	0	Neuston _L	—	23,08	2,15
SM 223	32°34,4'	29°13,1'	2133	2157–2301	2338	23.6.79	2380	670	RMT _M	BT-53	22,92	3,27
SM 224	32°33,4'	29°09,2'	0023	0044–0147	0216	24.6.79	2030	663–600	RMT _M	BT-53	22,90	3,59
SM 225S	32°20,4'	28°59,3'	—	0605–0611	—	24.6.79	—	38	Bongo	BT-54	22,10	1,95
SM 225D	32°20,4'	28°59,3'	—	0615–0636	—	24.6.79	—	212	Bongo	BT-54	22,15	1,81
SM 225N	32°20,4'	28°59,3'	—	0643–0653	—	24.6.79	—	0	Neuston _L	—	22,12	2,58
SM 226	32°28,6'	28°58,8'	0855	0916–0947	1008	24.6.79	710–775	710–775	Heavy Dredge	BT-54	22,00	0,00
SM 227	32°32,1'	28°55,8'	1109	1141–1211	1243	24.6.79	775–790	775–790	Dbl. Beam Trawl	BT-55	21,99	0,67
SM 228	32°29,5'	28°57,1'	1518	1536–1609	1631	24.6.79	700–650	700–650	Heavy Dredge	BT-55	22,33	0,00
SM 229	32°27,8'	28°58,9'	1748	1806–1836	1900	24.6.79	670–740	670–740	Dbl. Beam Trawl	BT-56	22,59	0,00
SM 230S	32°30,6'	28°57,0'	—	1921–1928	—	24.6.79	630	38	Bongo	BT-56	22,58	1,73
SM 230D	32°30,6'	28°57,0'	—	1934–1956	—	24.6.79	630	172	Bongo	BT-56	22,64	1,88
SM 231	32°30,0'	28°54,8'	—	2015–2300	—	24.6.79	550	0	JDN _{NNL}	—	22,63	0,00

TABLE 5 (cont.)

Station No.	Position		Time		Date	Bottom Depth	Fishing Depth	Gear	Bathy-thermograph No.	Sea surface temp.	Ship's speed
	Latitude	Longitude	Start	Fishing End							
	°S	°E				m	m			°C	knots
SM 232	32°14,9'	29°10,4'	0709	0724-0755	—	25.6.79	620-560	Heavy Dredge	BT-57	22,20	0,00
SM 233	32°15,2'	29°09,8'	0857	0913-0943	1004	25.6.79	540-580	Dbl. Beam Trawl	BT-57	22,01	2,16
SM 234	32°15,0'	29°09,1'	1045	1100-1133	—	25.6.79	500-520	Dbl. Beam Trawl	BT-57	21,89	2,04
SM 235	32°16,2'	29°07,6'	1156	1213-1314	1336	25.6.79	480-510	Dbl. Beam Trawl	BT-58	21,83	1,55
SM 236	32°14,3'	29°11,6'	1538	1603-1633	1657	25.6.79	670-660	Heavy Dredge	BT-58	21,89	0,00
SM 237	32°15,4'	29°09,7'	1724	1744-1813	1840	25.6.79	600-650	Dbl. Beam Trawl	BT-58	21,92	1,51
SM 238S SM 238N	32°14,5' 32°14,5'	29°00,4' 29°00,4'	— —	1955-2001 2020-2029	— —	25.6.79 25.6.79	100 100	Bongo NeustonL	BT-59 —	21,97 21,85	1,82 3,36
SM 239	32°14,8'	29°00,8'	2048	2052-2118	2133	25.6.79	90	Dbl. Beam Trawl	BT-59	21,81	2,05
SM 240	32°15,0'	28°58,8'	—	2200-2400	—	25.6.79	88	JDNNL	—	21,71	0,00
SM 241D	31°56,4'	29°27,5'	—	0601-0620	—	26.6.79	920	Bongo	BT-60	21,05	1,05
SM 242	31°54,8'	29°20,6'	—	1000-1300	—	26.6.79	82	Hand	—	20,64	0,00

SM 244S SM 244D	32°01,6' 32°01,6'	29°28,7' 29°28,7'	— —	0604-0607 0614-0633	27,6.79 27,6.79	1000 1000	172	Bongo Bongo	BT-61 BT-61	19,88 19,88	1,74 1,85
SM 245	32°00,7'	29°33,0'	0729	0806-0821	0912	27,6.79	1420	Heavy Dredge	BT-61	19,72	0,00
SM 246	31°58,6'	29°35,6'	0924	1006-1027	1114	27,6.79	1660-1640	Biol. Dredge	BT-61	19,70	0,00
SM 247	31°55,1'	29°38,8'	1301	1352-1415	1519	27,6.79	1800-1950	Biol. Dredge	BT-61	19,55	0,00
SM 248	31°56,9'	29°38,1'	1534	1631-1703	1828	27,6.79	1730	Dbl. Beam Trawl	BT-62	19,64	0,58
SM 249S SM 249D	31°58,8' 31°58,8'	29°24,6' 29°24,6'	— —	2039-2045 2049-2108	— —	27,6.79 27,6.79	450 450	Bongo Bongo	BT-62 BT-62	20,33 20,49	1,69 1,65
SM 250	31°59,3'	29°22,5'	2132	2140-2142	2202	27,6.79	c. 150-200	Heavy Dredge	BT-62	20,85	0,00
SM 251	31°56,0'	29°24,6'	—	2300-0100	—	27,6.79	137	JDNLL	—	21,31	0,00
SM 252S SM 252D SM 252N	31°44,8' 31°44,8' 31°44,8'	29°37,1' 29°37,1' 29°37,1'	— — —	0600-0605 0612-0626 0635-0646	— — —	28,6.79 28,6.79 28,6.79	650 650 650	Bongo Bongo NeustonL	BT-63 BT-63 —	21,35 21,35 21,34	1,68 1,63 2,68
SM 253	31°44,6'	29°41,2'	0739	0809-0828	0907	28,6.79	1010	Heavy Dredge	BT-63	21,23	0,00
SM 254	31°42,6'	29°40,4'	0928	1016-1047	1136	28,6.79	860-850	Dbl. Beam Trawl	BT-63	21,18	0,23
SM 255	31°37,8'	29°40,8'	1257	1302-1305	1311	28,6.79	125	Heavy Dredge	—	21,55	0,00
SM 256	31°37,2'	29°41,7'	1325	1330-—	—	28,6.79	105	Dbl. Beam Trawl	—	—	—

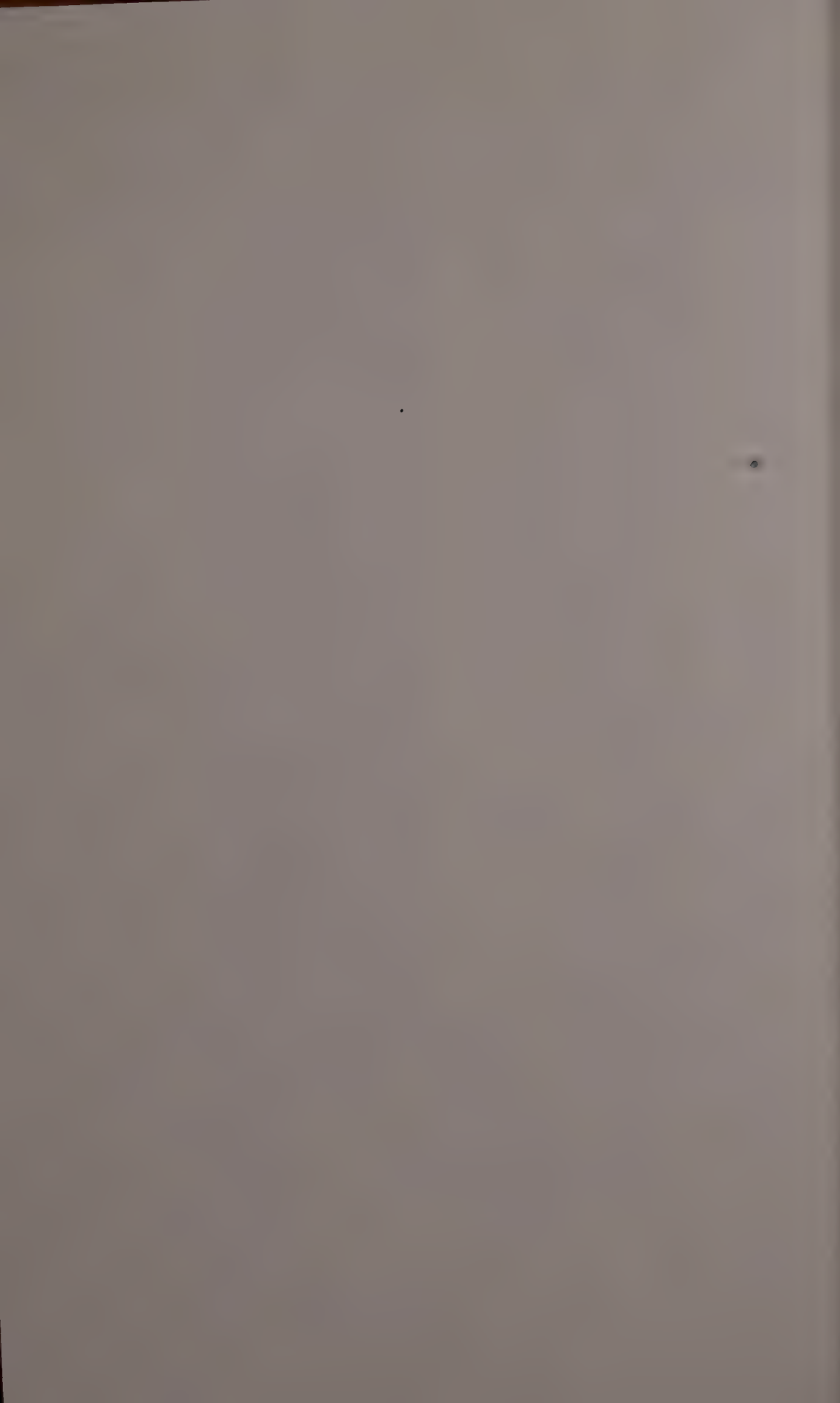


TABLE 5 (cont.)

Station No.	Position		Time			Date	Bottom Depth	Fishing Depth	Gear	Bathy-thermo-graph No.	Sea surface temp.	Ship's speed
	Latitude	Longitude	Start	Fishing	End							
	°S	°E					m	m			°C	knots
SM 232	32°14,9'	29°10,4'	0709	0724-0755	—	25.6.79	620-560	620-560	Heavy Dredge	BT-57	22,20	0,00
SM 233	32°15,2'	29°09,8'	0857	0913-0943	1004	25.6.79	540-580	540-580	Dbl. Beam Trawl	BT-57	22,01	2,16
SM 234	32°15,0'	29°09,1'	1045	1100-1133	—	25.6.79	500-520	500-520	Dbl. Beam Trawl	BT-57	21,89	2,04
SM 235	32°16,2'	29°07,6'	1156	1213-1314	1336	25.6.79	480-510	480-510	Dbl. Beam Trawl	BT-58	21,83	1,55
SM 236	32°14,3'	29°11,6'	1538	1603-1633	1657	25.6.79	670-660	670-660	Heavy Dredge	BT-58	21,89	0,00
SM 237	32°15,4'	29°09,7'	1724	1744-1813	1840	25.6.79	600-650	600-650	Dbl. Beam Trawl	BT-58	21,92	1,51
SM 238S	32°14,5'	29°00,4'	—	1955-2001	—	25.6.79	100	53	Bongo	BT-59	21,97	1,82
SM 238N	32°14,5'	29°00,4'	—	2020-2029	—	25.6.79	100	0	Neuston _L	—	21,85	3,36
SM 239	32°14,8'	29°00,8'	2048	2052-2118	2133	25.6.79	90	90	Dbl. Beam Trawl	BT-59	21,81	2,05
SM 240	32°15,0'	28°58,8'	—	2200-2400	—	25.6.79	88	0	JDNNL	—	21,71	0,00
SM 241D	31°56,4'	29°27,5'	—	0601-0620	—	26.6.79	920	212	Bongo	BT-60	21,05	1,05
SM 242	31°54,8'	29°20,6'	—	1000-1300	—	26.6.79	82	82	Hand Lines	—	20,64	0,00
SM 243	31°50,2'	29°25,1'	—	2100-2300	—	26.6.79	92	0	JDNNL	—	20,63	0,00
SM 244S	32°01,6'	29°28,7'	—	0604-0607	—	27.6.79	1000	53	Bongo	BT-61	19,88	1,74
SM 244D	32°01,6'	29°28,7'	—	0614-0633	—	27.6.79	1000	172	Bongo	BT-61	19,83	1,85
SM 245	32°00,7'	29°33,0'	0729	0806-0821	0912	27.6.79	1420	1420	Heavy Dredge	BT-61	19,72	0,00
SM 246	31°58,6'	29°35,6'	0924	1006-1027	1114	27.6.79	1660-1640	1660-1640	Biol. Dredge	BT-61	19,70	0,00
SM 247	31°55,1'	29°38,8'	1301	1352-1415	1519	27.6.79	1800-1950	1800-1950	Biol. Dredge	BT-61	19,55	0,00
SM 248	31°56,9'	29°38,1'	1534	1631-1703	1828	27.6.79	1730	?1730	Dbl. Beam Trawl	BT-62	19,64	0,58
SM 249S	31°58,8'	29°24,6'	—	2039-2045	—	27.6.79	450	53	Bongo	BT-62	20,33	1,69
SM 249D	31°58,8'	29°24,6'	—	2049-2108	—	27.6.79	450	212	Bongo	BT-62	20,49	1,65
SM 250	31°59,3'	29°22,5'	2132	2140-2142	2202	27.6.79	c. 150-200	c. 150-200	Heavy Dredge	BT-62	20,85	0,00
SM 251	31°56,0'	29°24,6'	—	2300-0100	—	27.6.79	137	137	JDNNL	—	21,31	0,00
SM 252S	31°44,8'	29°37,1'	—	0600-0605	—	28.6.79	650	53	Bongo	BT-63	21,35	1,68
SM 252D	31°44,8'	29°37,1'	—	0612-0626	—	28.6.79	650	212	Bongo	BT-63	21,35	1,63
SM 252N	31°44,8'	29°37,1'	—	0635-0646	—	28.6.79	650	0	Neuston _L	—	21,34	2,68
SM 253	31°44,6'	29°41,2'	0739	0809-0828	0907	28.6.79	1010	1010	Heavy Dredge	BT-63	21,23	0,00
SM 254	31°42,6'	29°40,4'	0928	1016-1047	1136	28.6.79	860-850	860-850	Dbl. Beam Trawl	BT-63	21,18	0,23
SM 255	31°37,8'	29°40,8'	1257	1302-1305	1311	28.6.79	125	125	Heavy Dredge	—	21,55	0,00
SM 256	31°37,2'	29°41,7'	1325	1330- —	—	28.6.79	105	—	Dbl. Beam Trawl	—	—	—

TABLE 6
Temperatures at selected depths, as obtained from bathythermograph profiles during the fifth cruise.

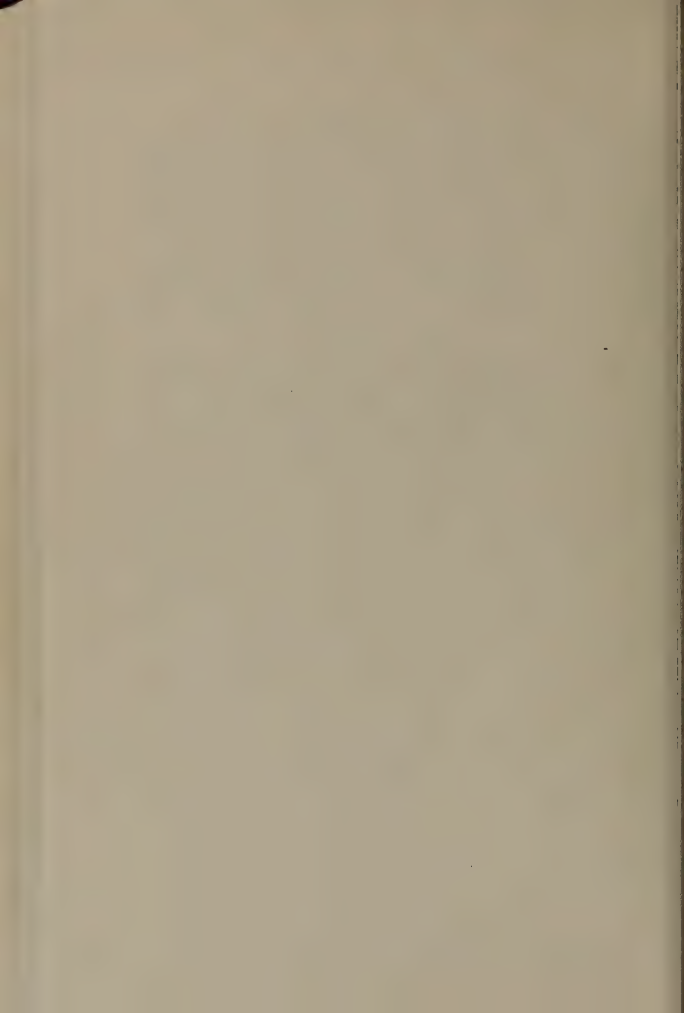
Depth	*0 m	10 m	20 m	30 m	40 m	50 m	60 m	70 m	75 m	100 m	200 m	300 m	400 m	500 m	600 m	700 m	800 m	900 m	1 000 m
Bathy-thermo-graph No.	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C	Temp. °C
BT-38	22.40	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
BT-39	23.91	23.15	23.14	23.14	23.12	22.77	22.25	21.22	20.90	18.83	15.05	13.08	11.63	10.73	9.59	8.70	7.22	6.02	4.80
BT-40	23.00	23.04	22.99	22.45	21.36	20.86	19.57	17.78	17.44	16.74	14.32	12.07	10.93	9.82	8.83	8.00	6.26	4.91	4.42
BT-41	22.94	22.98	22.92	22.96	22.33	21.28	20.68	18.22	17.61	16.68	14.34	11.92	10.87	9.74	8.75	7.69	6.29	4.92	4.37
BT-42	22.70	22.82	22.82	22.80	22.33	20.68	18.73	17.32	17.11	16.46	13.71	12.00	11.13	10.01	8.85	7.86	6.25	4.98	4.55
BT-43	22.73	22.59	21.97	20.89	20.40	19.60	17.80	16.94	16.66	16.17	14.02	11.78	10.87	9.73	8.71	7.50	5.93	4.85	4.39
BT-44	23.31	23.20	23.18	22.80	22.17	20.53	19.31	19.18	19.04	17.27	13.86	12.23	11.13	10.10	8.91	7.50	5.74	5.04	4.56
BT-45	22.80	22.53	22.52	21.76	20.44	19.02	18.21	17.40	17.18	16.17	13.68	12.23	11.30	10.50	9.50	7.87	6.30	5.27	4.66
BT-46	23.34	23.40	23.34	23.33	23.32	23.30	21.91	20.92	20.49	19.01	15.50	12.54	11.30	10.50	9.50	7.87	6.30	5.27	4.66
BT-47	23.25	22.78	22.78	22.47	21.93	20.42	19.96	19.42	18.80	16.41	13.69	12.40	11.11	10.05	—	—	—	—	—
BT-48	22.83	22.70	22.69	22.64	22.50	21.59	20.55	19.22	18.70	17.36	14.36	13.11	11.76	10.67	8.88	7.40	6.06	5.17	4.57
BT-49	23.18	23.23	23.21	23.20	23.19	22.36	20.69	19.90	19.60	18.03	14.84	13.45	12.08	10.39	9.03	7.47	6.28	5.10	—
**BT-52	23.07	23.10	23.11	23.11	23.11	22.08	20.73	19.85	19.70	18.62	15.12	13.46	11.94	10.43	8.92	7.04	5.68	5.00	4.43
BT-53	22.98	23.16	23.16	23.15	23.13	20.84	19.56	19.16	18.80	17.69	14.67	13.17	11.43	9.90	8.74	7.11	—	—	—
BT-54	22.12	22.08	21.81	19.43	18.59	17.38	16.88	16.52	16.46	15.73	13.49	12.20	10.14	9.20	—	—	—	—	—
BT-55	22.02	22.14	20.70	19.72	19.05	18.41	17.75	17.31	17.19	16.41	13.62	12.44	11.03	9.52	8.08	6.95	—	—	—
BT-56	22.66	22.49	22.30	21.30	20.35	18.67	18.06	17.42	17.25	16.30	13.51	—	—	—	—	—	—	—	—
BT-57	22.10	21.50	18.84	17.82	17.20	16.81	16.47	16.16	16.07	15.56	13.80	12.06	11.92	9.09	—	—	—	—	—
BT-58	21.85	21.93	19.30	18.29	17.58	17.47	16.76	16.34	16.28	15.63	14.14	12.22	—	—	—	—	—	—	—
BT-59	21.85	21.63	19.12	17.73	16.88	16.06	15.50	—	—	—	—	—	—	—	—	—	—	—	—
BT-60	21.05	21.01	21.01	17.70	16.00	15.18	14.92	14.79	14.71	14.01	13.04	11.72	10.83	9.00	—	—	—	—	—
BT-61	19.80	19.75	19.76	19.76	19.70	16.83	16.50	15.83	15.66	15.00	13.13	11.81	10.30	9.20	8.21	6.78	5.46	4.85	4.42
BT-62	20.20	21.68	21.68	21.68	21.67	19.76	17.25	17.16	17.00	16.71	15.42	—	—	—	—	—	—	—	—
BT-63	21.40	21.77	21.77	21.76	21.74	19.30	17.70	17.12	17.10	16.76	15.36	14.50	12.32	11.12	—	—	—	—	—

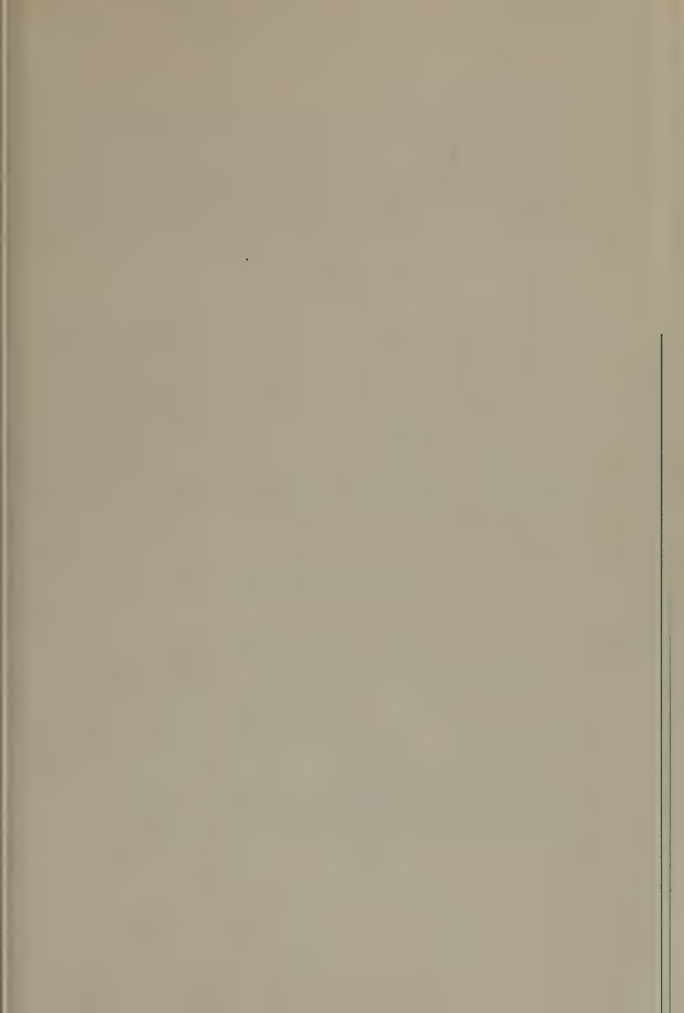
ACKNOWLEDGEMENTS

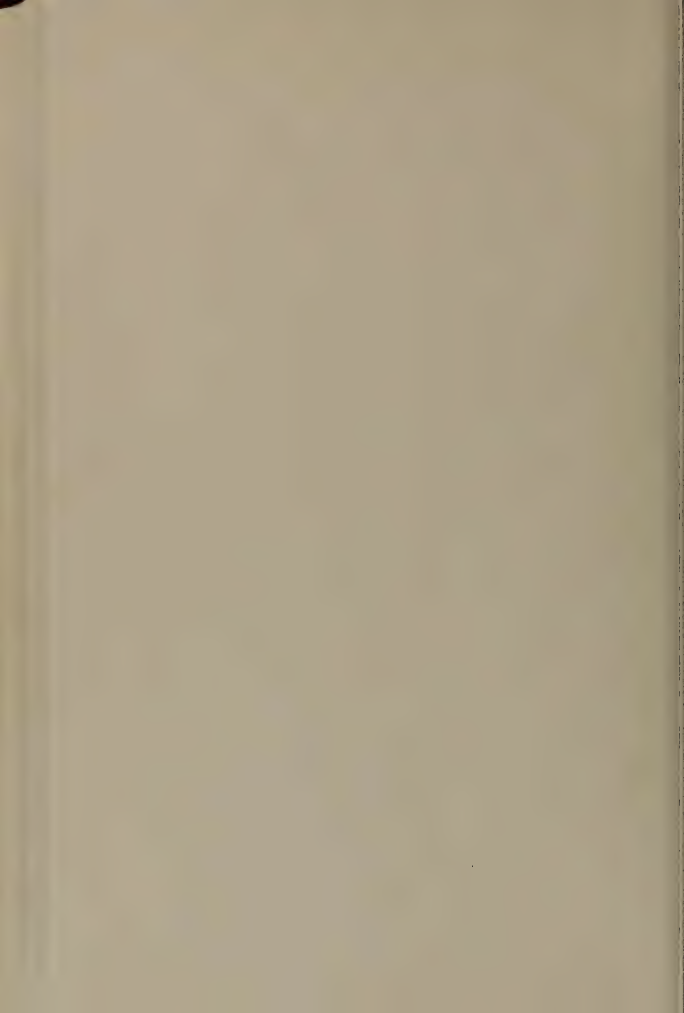
The South African Museum thanks the following organizations and individuals for their help during this programme: Government of Republic of Transkei for permission to fish in territorial waters; South African National Council for Oceanographic Research for financial assistance; Sea Fisheries Branch, Oceanographic Research Institute, East London Museum, Captain G. Foulis and crew of the *Meiring Naude*, Messrs P. Slevin and D. M. Pim (National Research Institute of Oceanology), Prof. M. M. Smith and Dr. P. C. Heemstra (J. L. B. Smith Institute of Ichthyology), Mr G. B. Ross (Port Elizabeth Museum), and Dr B. Kensley (U.S. National Museum of Natural History). Mr V. Branco (South African Museum) prepared Figure 1.

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6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14-15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a-b).

Nucula langillerti Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8-9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

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Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title; it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

ELIZABETH LOUW

THE SOUTH AFRICAN MUSEUM'S
MEIRING NAUDE CRUISES
PART 10
STATION DATA 1977, 1978, 1979

VOLUME 81 PART 6

AUGUST 1980

ISSN 0303-2515

507.68

ANNALS

OF THE SOUTH AFRICAN
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 Author's name(s)
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 Number of illustrations (figures, enumerated maps and tables, in this order)
- (b) *Abstract of not more than 200 words, intelligible to the reader without reference to the text*
- (c) *Table of contents giving hierarchy of headings and subheadings*
- (d) *Introduction*
- (e) *Subject-matter of the paper, divided into sections to correspond with those given in table of contents*
- (f) *Summary, if paper is lengthy*
- (g) *Acknowledgements*
- (h) *References*
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The number of the figure should be lightly marked in pencil on the back of each illustration.

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(b) Full references at the end of the paper, arranged alphabetically by names, chronologically within each name, with suffixes *a*, *b*, etc. to the year for more than one paper by the same author in that year, e.g. Smith (1969a, 1969b) and not Smith (1969, 1969a).

For books give title in italics, edition, volume number, place of publication, publisher.

For journal article give title of article, title of journal in italics (abbreviated according to the *World list of scientific periodicals*, 4th ed. London: Butterworths, 1963), series in parentheses, volume number, part number (only if independently paged) in parentheses, pagination (first and last pages of article).

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- BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
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(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume 81 Band
August 1980 Augustus
Part 6 Deel



THE UMZAMBA FORMATION AT ITS TYPE
SECTION, UMZAMBA ESTUARY (PONDOLAND,
TRANSKEI), THE AMMONITE CONTENT AND
PALAEOGEOGRAPHICAL DISTRIBUTION

By

HERBERT CHRISTIAN KLINGER

&

WILLIAM JAMES KENNEDY

Cape Town Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

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Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na gelang van die
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Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad 8000

OUT OF PRINT/UIT DRUK

1, 2(1-3, 5-8), 3(1-2, 4-5, 8, t.-p.i.), 5(1-3, 5, 7-9),
6(1, t.-p.i.), 7(1-4), 8, 9(1-2, 7), 10(1-3),
11(1-2, 5, 7, t.-p.i.), 15(4-5), 24(2), 27, 31(1-3), 32(5), 33

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Kopieregnavrae aan die Suid-Afrikaanse Museum

ISBN 0 908407 93 9

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

THE UMZAMBA FORMATION AT ITS TYPE SECTION, UMZAMBA ESTUARY (PONDOLAND, TRANSKEI), THE AMMONITE CONTENT AND PALAEOGEOGRAPHICAL DISTRIBUTION

By

HERBERT CHRISTIAN KLINGER

South African Museum, Cape Town

&

WILLIAM JAMES KENNEDY

Geological Collections, University Museum, Oxford

(With 5 figures and 3 tables)

[MS. accepted 6 December 1979]

ABSTRACT

Detailed collecting at the type section was undertaken to determine the exact age of the Formation and to determine whether more than one faunal zone is present. Faunal analysis based on ammonites shows that the age of the Formation at the type section ranges from Middle Santonian to Lower Campanian. The ammonoid faunas at the type section of the Umzamba Formation in Pondoland were compared with those of the False Bay region of Zululand, and it was found that certain morphotypes, e.g. oxycones, compressed evolute forms, and serpenticones are more dominant in the shallower water transgressive environment of Pondoland, presumably as a reflection of different living conditions in the two areas.

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INTRODUCTION

Although the presence of Cretaceous sediments in the vicinity of the Umzamba River Estuary (Pondoland, Transkei) has been known since at least 1824, the exact age and the question of whether or not a succession of distinct faunal associations is recognizable have long been disputed (Baily 1855; Griesbach 1871; De Grossouvre 1901; Rogers & Schwarz 1902; Woods 1906; Du Toit 1912, 1920, 1954; Van Hoepen 1920, 1921, 1965; Plows 1921; Spath 1921*b*, 1922, 1953; Rennie 1930; Haughton 1963, 1969; Kennedy & Klinger

1975). On the basis of the fauna and flora described by Baily (1855), Griesbach (1871), Chapman (1904, 1923), Woods (1906), Lang (1906), Broom (1907), Spath (1921a, 1921b), Van Hoepen (1920, 1921, 1965), Rennie (1930, 1935), Smutter (1956), Little (1957), Mädél (1960), Müller-Stoll & Mädél (1962), Dingle (1969), and Kennedy & Klinger (1977a, 1977b 1979), ages varying from Albion to Maastrichtian were postulated, the prevalent idea being that the Formation was of Senonian age (i.e. Coniacian to Campanian).

Failure to arrive at a decisive conclusion may be ascribed mainly to lack of precise stratigraphic control, and/or lack of current knowledge of the systematic affinities and stratigraphic ranges of some of the fossil taxa.

Aided by the extensive monographical studies of the Madagascar ammonoid faunas by Collignon (1928 onwards), his series *Atlas des fossiles caractéristiques de Madagascar (ammonites)*, and by the authors' preliminary biozonation for southern Africa (Kennedy & Klinger 1975), a new attempt was made to fill this gap in our current knowledge. For this purpose a detailed sampling programme was undertaken by one of the authors (H.C.K.) in 1974. However, due to circumstances beyond the authors' control, results of this investigation could not be published earlier and consequently parts thereof were disclosed elsewhere (Klinger & Kennedy 1977; Cooper 1977).

Finally, the apparent faunal differences between northern Zululand and Pondoland are examined briefly to determine their extent and probable causes.

DESCRIPTION OF THE EXPOSURES

Descriptions of the exposures at and near the Umzamba Estuary are provided in varying degrees of detail by Garden (1855), Griesbach (1871), Rogers & Schwarz (1902), Du Toit (1912, 1920), Plows (1921), Gevers (*in* Rennie 1930) and Kennedy & Klinger (1975), that of Plows (1921) being the most complete. Apart from details of the ammonoid succession at the type section, little else can be added to these general accounts. The lithologies encountered may be described briefly as follows:

The Cretaceous strata overlie Ordovician? quartzites belonging to the Table Mountain Group unconformably with a slight seaward dip of the order of two to four degrees. The basal beds are conglomeratic, consisting of abundant sandstone and lydianite pebbles set in an arenaceous matrix. Large logs, chelonian scutes and other reptilian remains, comminuted shell material, selachian teeth, and baculitid ammonites are locally common in these basal beds. Higher up in the sequence, lithologies become finer-grained, consisting essentially of alternating layers of grayish-green, fine-grained silts, and coarser-grained, shelly or sandy concretionary horizons. Some of the concretionary layers show traces of cross-bedding and scouring. Both silts and concretionary layers yield abundant fossils, and sections of gigantic inoceramids, more than a metre in diameter, are conspicuous. Fossils in the silty horizons are generally preserved as internal moulds, whereas those in the concretionary horizons retain

the original shell material. The majority of ammonites extracted from the concretionary horizons were embedded horizontally.

The most complete exposure is on the northern side of the estuary (Figs 1–2), named the Umzamba Cliff by Plows (1921, pl. 8 (fig. 3)). This is Gevers's (in Rennie 1930) 'first locality' and the authors' (Kennedy & Klinger 1975) locality 1. Griesbach's (1871, fig. 5) locality was probably taken about 100 m north-east of here (Fig. 3). Details of the section here vary considerably due to landslides and heavy surf action at the base of the cliff (see Rogers & Schwarz 1902: 40; Plows 1921: 60).

The Umzamba Cliff is here referred to as locality A (see Figs 3–4). Beds A3 and A7 are the levels of the prominent caves remarked upon by the early workers. These result from the collapse of the soft, silty beds between hard, concretionary layers. Horizons below Bed A8 can be easily reached from the base of the cliff by climbing on rubble from landslips. Higher horizons can be reached by scaling the cliffs or by taking a footpath over the top of the hill and then climbing down the cliff (see also Gevers 1977 for anecdotal details).

During low tide, foreshore platforms are exposed north-east of locality A for more than a kilometre along the beach. Due to the abundance of silicified tree trunks, this locality is known as the 'Petrified Forest' and is indicated as such on tourist and topographic maps. Most of the larger logs appear to be orientated in an east-north-east direction, presumably paralleling the Cretaceous shoreline. The exposures are in horizons below those seen at locality A, and are here referred to as locality B.

Locality C is situated on the southern side of the estuary (Plow's 1921 Right Bank), and extends for some distance along the coast, but the latter is only poorly exposed at low tide (see Rogers & Schwarz 1902: 40). Strata even lower down in the succession than those found at locality A and B are exposed here, but the actual contact with the underlying basement rocks was not exposed during the authors' visits. Large boulders of quartzite derived from the Ordovician? Table Mountain Group are exposed on the NW side of the estuary, but one or two metres of sand covered the actual contact. Approximately 10 m of sediment are exposed at locality C. The highest bed, Bed C11, probably corresponds to Bed 3 at locality A.

THE AGE OF THE UMZAMBA FORMATION

In determining the age of the Umzamba Formation at the type section, the ammonoid zonation compiled for Madagascar by Collignon (1966, 1969) and the provisional one compiled for Natal and Zululand by the authors in a slightly modified form (Kennedy & Klinger 1975) (Tables 1 and 2 respectively) are employed.

The base of the section

The lowermost fossiliferous units are Bed C4 and the foreshore outcrops in the northern part of locality B. Occasional *Baculites capensis* Woods, rare

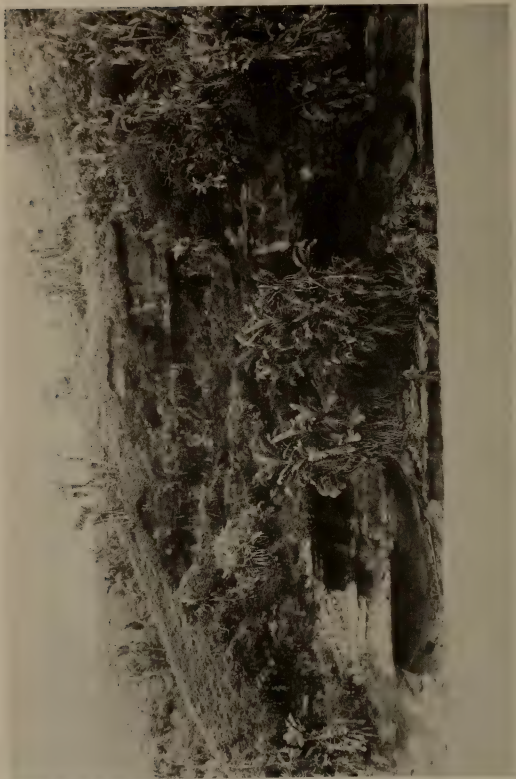


Fig. 1. The main exposure at Umzamba, Umzamba Cliff, photographed in 1974.
Mr Johannes Nonyane is at the foot of the cliff for scale.

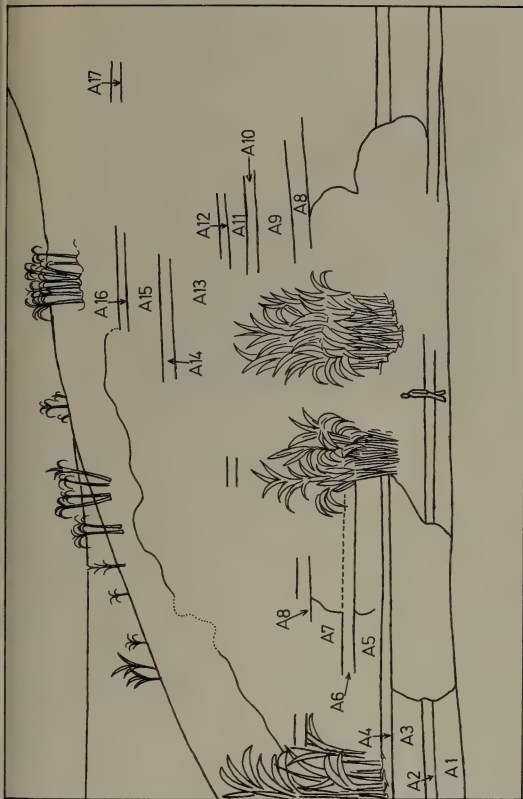


Fig. 2. Drawing of Umzamba Cliff to illustrate units as referred to in the text and in Figure 4.



Fig. 3. Section at Umzamba about 100 m to the north of the main exposure shown in Figure 1. This appears to be the site on which Griesbach (1871 (fig. 5)) based his section.

Gaudryceras varicostatum Van Hoepen, *Texanites umzambiense* Klinger & Kennedy and *Scaphites* sp. occur here.

The authors had originally considered (Kennedy & Klinger 1971, 1975) that the base of the Umzamba Formation was of Coniacian age on the basis of the reference of *Muniericeras cricki* Spath (1921b, 1922) (of which *Barroisiceras umzambiense* van Hoepen 1965 (Fig. 7A) is a synonym) to the Coniacian collignoniceratid genus *Subprionotropis*. Since most of the above listed species are typically Santonian forms, this determination became open to question, and the authors would now suggest that this species is better referred to the homoeomorphic genus *Lehmaniceras* Collignon, 1966 (see also Klinger & Kennedy 1977: 103; Cooper 1977: 16). Van Hoepen's specimen was collected from an unrecorded horizon on the southern side of the Umzamba Estuary at locality C. Apart from Pondoland, *Lehmaniceras* is known only from Madagascar where it is relatively abundant in the Middle Santonian.

The association of *Texanites umzambiense* Klinger & Kennedy with *Baculites capensis* Woods is related to that of *Plesiotexanites olivetiforme* Klinger & Kennedy and *Baculites capensis* occurring in the first division of the Santonian in Zululand. In Madagascar, *Baculites capensis* occurs in the Lower

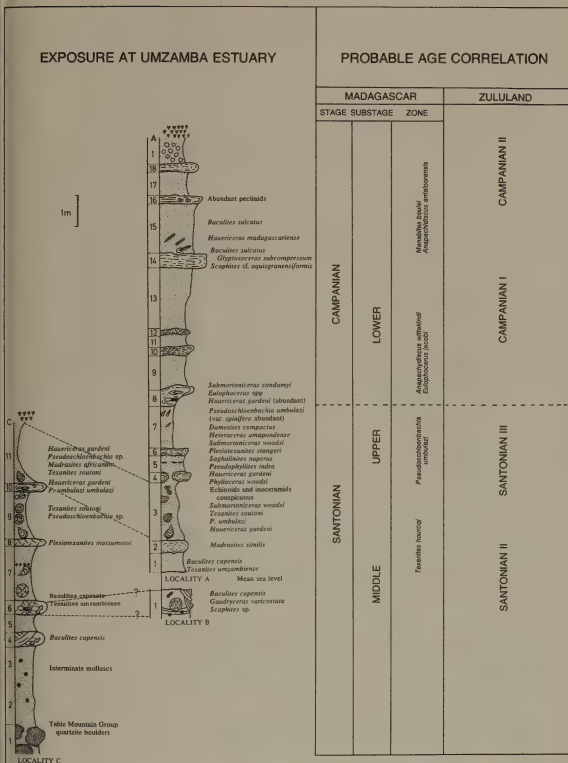


Fig. 4. Stratigraphic section at Umzamba, including Umzamba Cliff, here marked A, the foreshore beach exposures north of A, here marked as B, and the section on the southern side of the estuary, here marked C.

TABLE 2

Provisional ammonoid succession for Natal and Zululand as compiled by the authors (1975), here presented in slightly modified form to accommodate new data.

CAMPANIAN II	<p><i>Menabites (Australiella)</i> abundant in lower part. Some appear to range throughout together with <i>Bevahites</i> spp. <i>Baculites sulcatus</i> is abundant throughout while pachydiscids become common in the higher part, e.g. <i>A. wittekindi</i>, <i>A. arrialoorensis</i></p>
CAMPANIAN I	<p><i>Submortonicer</i> <i>woodsii</i> and related forms are common; other ammonites include <i>Bevahites</i> and <i>Menabites</i>, <i>Hauericeras gardeni</i>, <i>Pseudoschloenbachia</i>, <i>Bostrychoceras</i> and diplomoceratids.</p> <p>The local base of the stage is drawn below the level of abundant <i>Submortonicer</i></p>
SANTONIAN III	<p><i>Hauericeras gardeni</i> is abundant; the remainder of the fauna is as in Santonian II and is relatively scarce.</p>
SANTONIAN II	<p>Abundant <i>Plesioteanaxites stangeri</i> and varieties, <i>Texanites soutoni</i>, <i>Texanites</i> spp., <i>Hauericeras</i> and <i>Pseudoschloenbachia</i> occur, as do <i>Eupachydiscus</i>? <i>Hyphantoceras</i> and diplomoceratids</p>
SANTONIAN I	<p><i>Texanites oliveti</i>, <i>Plesioteanaxites stangeri densicosta</i> and <i>sparsicosta</i>, <i>Hauericeras gardeni</i>, <i>Pseudoschloenbachia</i> sp <i>Pseudophyllites indra</i>, <i>Karapadites</i>?, <i>Eupachydiscus</i>? sp., <i>Gaudryceras</i> spp., <i>Hyphantoceras</i> sp. and diplomoceratids.</p> <p>The base of the stage is drawn at the level of the appearance of <i>Texanites</i> <i>sensu strictu</i> in numbers</p>
CONIACIAN V	<p>Abundant baculitids ornamented only by growth striae. Also ammonites resembling <i>Pseudoschloenbachia primitiva</i> Collignon and <i>Scaphites</i>.</p>

and Middle Santonian. *Gaudryceras varicostatum* occurs as low as the second division of the Coniacian of Zululand, but is also recorded from the Lower Santonian of Madagascar (Collignon 1966: 3).

On the basis of these ranges, it seems quite certain that the basal beds are of Santonian age, and probably uppermost Lower to Middle Santonian in the sense of Collignon (1966) and equivalent to the authors' first or second divisions, probably the latter, of the Zululand Santonian.

Top of the succession

The uppermost ammonite-bearing beds exposed, Beds A14 and A15 (probably the equivalent of Gevers's (in Rennie 1930) Bed T) yield *Baculites sulcatus* (Baily), *Hauericeras madagascariense* Collignon (Fig. 5B), *Glyptoxoceras subcompressum* (Forbes) and *Scaphites* cf. *aquisgranensisiformis* Collignon. *Hauericeras madagascariense* has a very restricted range in Madagascar, occurring only in the upper part of the Lower Campanian zone of *Menabites boulei* and *Apapachydiscus arrialoorensis* (see Collignon 1961, 1969; and Table 1 herein). Comparisons with Zululand at this interval are tenuous, but *Baculites sulcatus* is comparable with *Baculites vanhoepeni* Venzo, as discussed earlier (Klinger & Kennedy 1977: 73-74) and is indicative of the second division of the Campanian in Zululand. The absence of *Menabites* s.l. species which characterize this horizon in Zululand, however, is puzzling.

The uppermost exposed beds at the Umzamba Cliff are thus provisionally dated as uppermost Lower Campanian in the sense of Collignon (1969) and tentatively the second division of the Zululand Campanian *sensu* Kennedy & Klinger (1975).

Subdivision of the sequence

The ammonites collected *in situ* from the remainder of the sequence exposed at the Umzamba Estuary are shown in Figure 4. Apart from a thin zone of rolled and encrusted clay pebbles and hiatus concretions in Bed A5, which may represent a very short break in deposition, no evidence could be found of a major sedimentological interruption within the Umzamba Formation. It may thus be assumed that deposition was virtually continuous.

Bed A7 yields abundant *Pseudoschloenbachia umbulazi umbulazi* (Baily), *P. umbulazi* (Baily) *griesbachi* van Hoepen, and *P. umbulazi* (Baily) *spinifera* van Hoepen (all probably conspecific). All three 'subspecies' occur together, but *P. umbulazi spinifera* appears to become more abundant towards the top of the Bed. *Hauericeras gardeni* (Baily) is also very abundant. This association corresponds to the third division of the Santonian in Zululand, and the Upper Santonian zone of *Pseudoschloenbachia umbulazi* in Madagascar. *Eulophoceras tenue* van Hoepen, *E. umzambiense* van Hoepen and other *Eulophoceras* species (all probably conspecific) occur together with *Submortonicerias condamyi* near the contact of Beds A7 and A8. In Madagascar the base of the Campanian is drawn immediately below the first occurrence of *Eulophoceras*, whereas it is

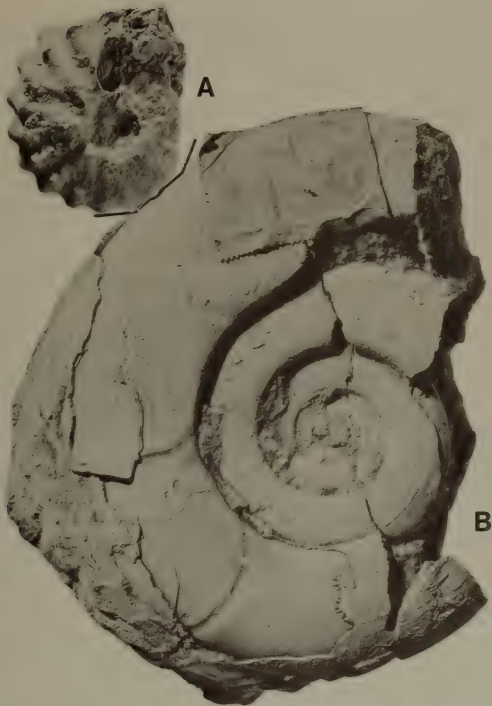


Fig. 5. A. *Lehmaniceras cricki* (Spath, 1921). (= The holotype of Van Hoepen's 1965: 161, pl. 6 and text-fig. 2a *Barroisiceras umzambiensis*. From the southern side of the Umzamba Estuary (herein locality C) at an unknown horizon (see Van Hoepen 1965: 162). Geological Survey SAS-P1093. $\times 1$.

B. *Hauericeras madagascariense* Collignon, 1961. This is the specimen collected by Gevers from his horizon 'T' at the Umzamba Cliff (herein locality A), probably horizon A15, being associated with specimens of *Baculites sulcatus* Bailey on reverse side. South African Museum SAM-7043. $\times 0.75$.

drawn in Zululand below the first occurrence of abundant *Submortonicer*as. It seems reasonable to draw the contact between the Santonian and Campanian Stages at the contact between Beds A7 and A8. It should be pointed out, however, that *Submortonicer*as appears slightly earlier in Pondoland than in Madagascar.

The paucity of ammonites from above Bed A7 at the type section appears to be due more to physical difficulties encountered in collecting in higher sections of the cliff rather than real differences.

Scaphites cf. *aquisgranensisformis* in Bed A14 is comparable with *S. aquisgranensisformis* Collignon, which occurs in the subzone of *Scaphites reesidei* at the boundary between the Zone of *Menabites boulei* and *Anapachydiscus arrialoorensis* and the Zone of *Karapadites karapadensis* of the Lower Campanian of Madagascar.

COMPARISON OF THE PONDOLAND AND ZULULAND AMMONOID FAUNAS

The authors (Klinger & Kennedy 1977: 104; 1980) and Spath (1921*b*: 53) had previously pointed to the apparent differences between the ammonoid faunas of Pondoland and those of biostratigraphically equivalent sediments further north at Umkwelane Hill and in the False Bay region of Zululand.

A detailed comparison of the faunas of Pondoland with those of Durban, Richards Bay, Umkwelane Hill, and Zululand must await a complete revision of all the ammonoid faunas, but preliminary results are given here in Table 3. The paucity of the faunas in the Durban and Richards Bay and to a lesser extent the Umkwelane Hill regions as shown in the table are primarily due to lack of sufficient exposures, rather than real differences. Furthermore, the absence of some Pondoland species in Zululand may be partially due to our inability to recognize the generally small Pondoland species as the nuclei of larger species occurring in Zululand. This latter discrepancy is not applicable to the Texanitinae, which generally grow to very large size, especially in Pondoland.

Despite these shortcomings, the picture that emerges is not one of total geographic separation, but rather one of concentration of certain shell morphotypes in specific areas. Very good examples of this are the oxyconic pseudoschloenbachiiids and *Eulophoceras* spp., the compressed evolute *Hauericeras gardeni* (Baily) and also the serpenticonic rounded *Plesiotexanites stangeri* (Baily). Examination of the Van Hoepen Pondoland collections in the Transvaal Museum (Pretoria) and personal collection at the type section, shows that *Pseudoschloenbachia* and *Hauericeras* can be counted by the thousands, as compared to numbers well below the hundreds in biostratigraphically equivalent strata in Zululand. Known specimens of *Eulophoceras* from Pondoland number about fifty, whereas the number from Zululand is well below ten. Similarly, only two tentative specimens of *Plesiotexanites stangeri* (Baily) are known from the False Bay region of Zululand, whereas it is relatively common in Pondoland.

TABLE 3

Distribution of ammonoid taxa at Umzamba, Durban, Richards Bay, Umkwelane Hill and northern Zululand.

Abbreviations used in Table

Absent (—)	Common (C) = 10-50
Rare (R) = 1-5	Abundant (A) = >100
Occasional (O) = 5-10	

SPECIES	FONDOLAND	DURBAN	RICHARDS BAY	UMKWELANE HILL	ZULULAND
<i>Phylloceras</i> (<i>H.</i>) <i>woodsii</i> <i>woodsii</i> van Hoepen	O	—	—	—	—
<i>Partschiceras umzambiense</i> (van Hoepen)	R	—	—	—	—
<i>Tetragonites superstes</i> van Hoepen	O	—	—	—	—
<i>Saghalinites cala</i> (Forbes)	R	—	—	—	—
<i>Saghalinites nuperus</i> (van Hoepen)	O	—	—	—	R
<i>Pseudophyllites indra</i> (Forbes)	R	—	—	—	R
<i>Pseudophyllites teres</i> (van Hoepen)	R	—	—	—	—
<i>Gaudryceras varicostatum</i> van Hoepen (= <i>G. cinctum</i> Spath 1922)	R	—	—	—	—
' <i>Gaudryceras</i> ' <i>sigcau</i> van Hoepen	R	—	—	—	—
<i>Anagaudryceras subsacya</i> (Marshall)	—	R	—	—	—
<i>Anagaudryceras subtilineatum</i> (Kossmat)	R	—	—	—	—
<i>Vertebrites kayei</i> (Forbes)	R	—	—	R	—
<i>Gaudryceras denseplicatum</i> (Jimbo) (= <i>amapondense</i> van Hoepen)	R	—	—	—	R
' <i>Heteroceras</i> ' <i>amapondense</i> van Hoepen	R	—	—	—	R-O
<i>Pseudoxybeloceras amapondense</i> van Hoepen	R	—	—	—	?
<i>Glyptoxoceras compressum</i> (Forbes)	R	—	R	—	R
<i>Hoploscaphtes</i> spp.	R-O	—	—	—	?
<i>Baculites capensis</i> Woods	O-C	O-C	O-C	O-C	A
<i>Baculites bailyi</i> Woods	O	—	—	C	A
<i>Baculites sulcatus</i> Baily	C	—	—	—	?
<i>Damesites compactum</i> van Hoepen	R	—	—	—	—
<i>Desmophyllites simplex</i> van Hoepen	R	—	—	—	—
<i>Desmophyllites crassa</i> (van Hoepen)	R	—	—	—	—
<i>Hauericeras gardeni</i> (Baily)	A	R	O	O-C	C
<i>Hauericeras madagascariense</i> Collignon	R	—	—	—	—
<i>Natalites</i> spp.	O-C	—	—	—	—
(including <i>N. natalensis</i> Spath, <i>N. acutico-</i> <i>status</i> Spath, <i>N. faku</i> van Hoepen, <i>N. africanus</i> van Hoepen, <i>N. similis</i> Spath)					
<i>Parapuzosia haughtoni</i> Spath	R	—	—	R	—
<i>Pachydiscus simplex</i> van Hoepen	R	—	—	—	—
<i>Pachydiscus umtafunensis</i> Spath	R	—	—	—	—
<i>Pachydiscus antecursor</i> van Hoepen	R	—	—	—	—
<i>Eulophoceras</i> spp.	O-C	?R	—	—	R
(including <i>Eulophoceras natalense</i> Hyatt, ' <i>Spheniscoceras</i> ' <i>africanum</i> Spath, 'S' <i>tenue</i> Spath, 'S' <i>minor</i> Spath, 'Pelecodiscus' <i>ama-</i> <i>pondense</i> van Hoepen, 'P' <i>umzambiense</i> van Hoepen)					
<i>Pseudoschloenbachia</i> spp.	A	—	O	O	O-C
(including <i>P. umbulazi</i> (Baily), <i>P. pseudo-</i> <i>fournieri</i> Spath, <i>P. papillata</i> Spath, <i>P. gries-</i> <i>bachi</i> Spath)					
<i>Texanites umzambiense</i> Klinger & Kennedy	R	—	—	—	—
<i>Texanites presoutoni</i> Klinger & Kennedy	R	—	—	—	R
<i>Texanites soutoni</i> (Baily)	C	—	R	R	C
<i>Texanites texanus</i> s. 1.	R	—	—	—	R
<i>Submortonicerus woodsii</i> (Spath)	R	R	R	R	O
<i>Submortonicerus condamyi</i> Collignon	R	—	—	—	O
<i>Plesiotelexanites stangeri</i> (Baily)	C	R	R	R	?R
<i>Plesiotelexanites matsumotoi</i> Klinger & Kennedy	R	—	—	—	—
<i>Lehmanicerus cricki</i> (Spath)	R	—	—	—	—

Other species, such as *Texanites soutoni* (Baily), *Submorticeras woodsi* (Spath) and *S. condamyi* (Collignon) are common to both areas, though subtle differences exist as discussed earlier (Klinger & Kennedy 1980) meriting separation at sub-specific level. In the smooth lytoceratid forms the picture is somewhat obscure due to limited numbers (Kennedy & Klinger 1977b). *Saghalinites nuperus* (van Hoepen) and *Pseudophyllites indra* (Forbes) are common to both Zululand and Pondoland, but are numerically superior in Pondoland. *Pseudophyllites teres* (Marshall) is poorly known and has so far been recorded from Pondoland only.

Phylloceratids are also restricted in numbers in Pondoland, but both known species, *Phylloceras* (*Hypophylloceras*) *woodsi woodsi* van Hoepen and *Partschiceras umzambiense* van Hoepen have so far not been recorded from the False Bay region of Zululand (Kennedy & Klinger 1977a).

Details on the pachydiscids are still in preparation but show no distinct trends, neither do the gaudryceratids (Kennedy & Klinger 1979).

Amongst the heteromorphs, *Baculites capensis* Woods and *B. bailyi* Woods are common to both Zululand and Pondoland, whereas the Pondoland species, *B. sulcatus* (Baily), has a possible equivalent in Zululand in *B. vanhoeffeni* Venzo (Klinger & Kennedy 1977). '*Heteroceras*' *amapondense* van Hoepen (= *Anaklinoceras stephensoni* Collignon 1966) is relatively rare, but is known from both areas, as also, apparently are species of *Pseudoxybeloceras* and *Glyptoxoceras*. The scaphitids have not been studied sufficiently for detailed analysis.

The fact that species such as *Texanites soutoni*, *Submorticeras woodsi*, *S. condamyi*, *Pseudoschloenbachia umbulazi* and *Hauericeras gardeni* occur in all major outcrop areas, ranging from Umzamba, through Durban, Richards Bay and Umkwelane Hill to the False Bay region of Zululand, clearly precludes the presence of an impenetrable physical barrier, and supports the authors' previous views (Klinger & Kennedy 1977: 104) of open marine connection between the areas. One of their previous views, however, that the biostratigraphically equivalent strata in Zululand were probably not well exposed (Klinger & Kennedy 1977: 104) now appears erroneous in view of the above data.

It has been suggested recently (see Cooper 1977: 32) that trophic resources increase during transgressions, which in turn leads to population explosions of certain favoured species. In the case of the diachronous southwards-extending Umzamba Formation Santonian transgression (Klinger & Kennedy 1977), these favoured species appear to be the oxyconic pseudoschloenbachiiids and *Eulophoceras* spp, the compressed evolute *Hauericeras gardeni* and the serpenticonic *Plesiotexanites stangeri*.

Due to the abundance of specimens, a high degree of splitting into various morphotypes was applied to species (see Van Hoepen 1921; Spath 1922). The authors would suggest that it will be possible to reduce the various 'species' or variants of *Pseudoschloenbachia* and *Eulophoceras* to a single species each, as has been done in the case of *Plesiotexanites stangeri* (Baily) (Klinger & Kennedy 1980).

(A comparable situation to that at Umzamba occurs in Zululand following the Lower Coniacian transgression (Kennedy & Klinger 1971). Here the sediments are dominated by the oxyconic *Proplacenticer* 'species' *P. umkwelanense* (Etheridge), *P. subkaffrarium* (Spath) and *P. kaffrarium* (Etheridge) and very evolute serpenticonic peroniceratids belonging to the groups of *Peroniceras tridorsatum* (Schlüter), *P. dravidicum* (Kossmat), *P. westphalicum* (Schlüter) etc. Klinger, *et al.* (in prep.) suggest that the *Proplacenticer* 'species' ranging from the completely smooth *P. umkwelanense* through *P. subkaffrarium* with undulating flanks to the distinctly umbilically spinose *P. kaffrarium* all belong to one variable species. A similar simplification of peroniceratid systematics is also envisaged.)

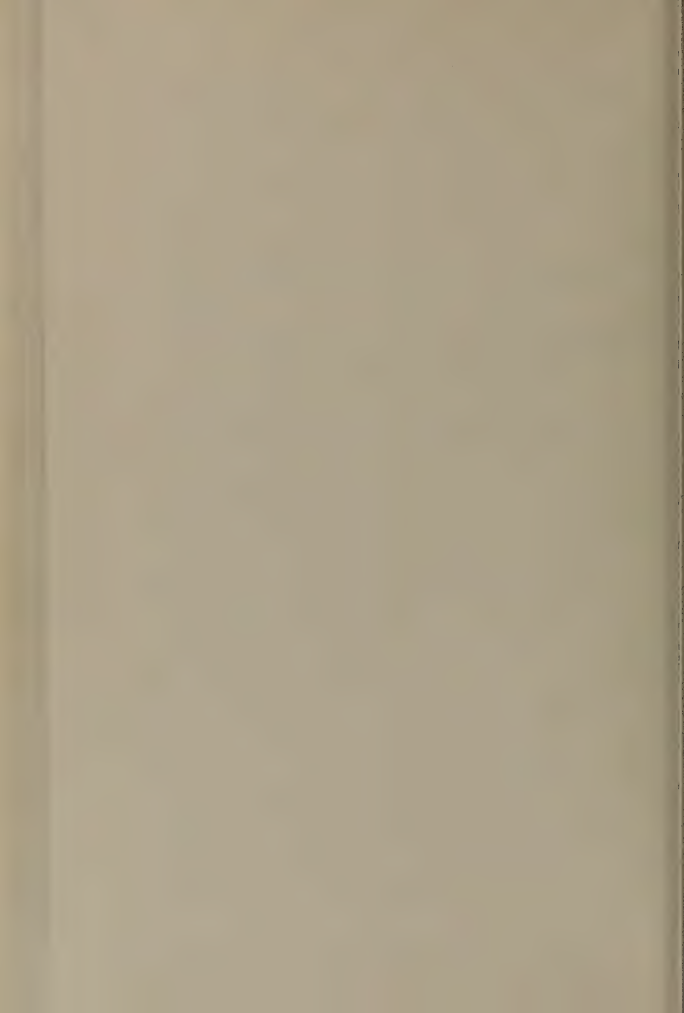
The question which now arises, and for which the authors can find no satisfactory answer, is why these particular morphotypes (oxycones, e.g. *Pseudoschloenbachia*; compressed evolute, e.g. *Hauericeras*; and serpenticone, e.g. *Plesiotexanites stangeri*) proved to be so successful in terms of numbers in a shallow-water, transgressive environment and tended towards a certain degree of endemism and great intraspecific variation.

The wide global distribution of *Plesiotexanites stangeri* (Klinger & Kennedy 1980) clearly shows that these forms were not restricted to transgressive habitats only and were capable of substantial dispersal, but apparently preferred a shallower water transgressive milieu. It may be suggested that the shell types were hydrodynamically suited to this particular type of environment, but again specific explanations are lacking.

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Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14–15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a–b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8–9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

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Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

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THE UMZAMBA FORMATION AT ITS TYPE
SECTION UMZAMBA ESTUARY (PONDOLAND,
TRANSKEI), THE AMMONITE CONTENT AND
PALAEOGEOGRAPHICAL DISTRIBUTION

VOLUME 81 PART 7

JUNE 1980

ISSN 0303-2515

507.68

ANNALS

OF THE SOUTH AFRICAN
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CAPE TOWN



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- BULLOUGH, W. S. 1960. *Practical invertebrate anatomy*. 2nd ed. London: Macmillan.
- FISCHER, P.-H. 1948. Données sur la résistance et de la vitalité des mollusques. *J. Conch.*, Paris 88: 100-140.
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(continued inside back cover)

ANNALS OF THE SOUTH AFRICAN MUSEUM
ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

Volume **81** Band
June **1980** Junie
Part **7** Deel



ENVIRONMENTAL AND ECOLOGICAL
IMPLICATIONS OF LARGE MAMMALS FROM
UPPER PLEISTOCENE AND HOLOCENE SITES
IN SOUTHERN AFRICA

By

RICHARD G. KLEIN

Cape Town · Kaapstad

The ANNALS OF THE SOUTH AFRICAN MUSEUM

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Obtainable from the South African Museum, P.O. Box 61, Cape Town 8000

Die ANNALE VAN DIE SUID-AFRIKAANSE MUSEUM

word uitgegee in dele op ongereelde tye na gelang van die
beskikbaarheid van stof

Verkrygbaar van die Suid-Afrikaanse Museum, Posbus 61, Kaapstad 8000

OUT OF PRINT/UIT DRUK

1, 2(1-3, 5-8), 3(1-2, 4-5, 8, t.-p.i.), 5(1-3, 5, 7-9),
6(1, t.-p.i.), 7(1-4), 8, 9(1-2, 7), 10(1-3),
11(1-2, 5, 7, t.-p.i.), 15(4-5), 24(2), 27, 31(1-3), 32(5), 33

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Kopieregnavrae aan die Suid-Afrikaanse Museum

ISBN 0 908407 91 2

Printed in South Africa by
The Rustica Press, Pty., Ltd.,
Court Road, Wynberg, Cape

In Suid-Afrika gedruk deur
Die Rustica-pers, Edms., Bpk.,
Courtweg, Wynberg, Kaap

ENVIRONMENTAL AND ECOLOGICAL IMPLICATIONS OF LARGE MAMMALS FROM UPPER PLEISTOCENE AND HOLOCENE SITES IN SOUTHERN AFRICA

By

RICHARD G. KLEIN

Department of Anthropology, University of Chicago

(With 5 figures, 7 tables and 1 appendix)

[MS. accepted 13 December 1979]

ABSTRACT

There are now more than seventy-five Upper Pleistocene and Holocene localities in southern Africa that have provided analysable remains of large mammals. The purpose of this paper is to summarize the information these remains have provided on past environments, on the evolution of man-environment relationships, and on the ecology and demise of extinct species.

For the purposes of discussion, the fossiliferous Upper Pleistocene and Holocene sites are divided among six modern southern African ecozones, distinguished from one another on climatic, phytogeographic, and zoogeographic grounds. Changes in large mammal distributions or in species frequencies that probably reflect Upper Pleistocene and Holocene environmental change can be demonstrated in all six ecozones, but a well-defined pattern of change in mammalian faunas that can be correlated with a pattern of long-term environmental change established on other grounds can be demonstrated in only one ecozone. This is the Cape Zone, where cooler intervals during the Upper Pleistocene repeatedly witnessed an increase in grazing ungulates relative to browsers. In part, the failure of comparable patterns to emerge in other zones may reflect the fact that Upper Pleistocene environmental and faunal change was greater in the Cape Zone than elsewhere, but in large part it almost certainly reflects the better overall quality of data from the Cape—more well-dated sites and more relatively large faunal assemblages for which detailed numerical data are available.

The greater quantity and higher quality of data from the Cape also make it the only ecozone in which there is a substantive basis to discuss: (i) long-term changes in human ability to obtain large mammals; and (ii) the reasons for the disappearance of several large mammal species which were common in various parts of southern Africa during the Upper Pleistocene. The Cape data suggest: (i) that Middle Stone Age people were less proficient hunter-gatherers than their Later Stone Age successors; and (ii) that a combination of environmental change and the greater hunting proficiency of Later Stone Age peoples was responsible for the large mammal extinctions.

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AIMS AND BASIC DEFINITIONS

As a result of research undertaken mainly in the 1960s and 1970s, there are now more than seventy-five Upper Pleistocene and Holocene localities in southern Africa that have provided analysable remains of large mammals. This paper aims to summarize the information these remains have provided on past environments, on the evolution of man-environment relationships, and on the ecology and demise of extinct species.

For the purposes of this paper, southern Africa is defined relatively broadly to include the Zambesian, Transvaalian, Kalaharian, Basutolian, Karoo-Namaqualian, and Cape Ecozones of Devred, as presented in De Vos (1975) (Fig. 1 here). The ecozones themselves are defined on the basis of climatic, phytogeographic, and zoogeographic features which are summarized below (based mainly on information in De Vos (1975) and Brown (1965)). The zones are of course abstractions in the sense that they grade into one another rather than being sharply bounded, and within each there is important climatic, phytogeographic, and zoogeographic variation, as determined for example by great differences in altitude, subsurface drainage, or proximity to permanent water. However, the zones clearly reflect gross differences in the historic distribution and relative abundance of large mammal species and therefore have definite value as a first basis for gauging the palaeoenvironmental significance of fossil mammal faunas.

In modern political terms, southern Africa, as defined here, comprises especially the countries of Angola, Zambia, Malawi, Mozambique, Zimbabwe Rhodesia, Botswana, South West Africa (Namibia), South Africa, Lesotho, and Swaziland. The approximate locations of the principal fossiliferous Upper Pleistocene and Holocene sites within these countries are shown in Figure 2, from which it is clear that the overwhelming majority are located in South Africa, South West Africa, Zimbabwe Rhodesia, and Zambia. In general, blank spots on the map reflect the absence of interested researchers as much or more than any other factor. Undoubtedly, many pertinent sites especially wait to be discovered or excavated in Angola, Botswana, Mozambique, and Malawi.

For the purposes of this paper, the Upper Pleistocene and Holocene have been taken to comprise the time interval represented by stages 1 through 5 of the



Fig. 1. Southern African ecozones, with the most prominent suid, bovid, and equid species found in each. The outlines and names of the zones are from De Vos (1975). Information on species distributions was obtained primarily from Ansell (1971a, 1971b), Ellerman *et al.* (1953), Joubert & Mostert (1975), Smithers (1966, 1971), and Smithers & Lobão Tello (1976).

deep-sea core oxygen-isotope stratigraphy, that is, approximately the last 130 000 years. These stages are listed in Table 1, along with the temperature conditions they are believed to reflect and their dates, in so far as these have been established. In conventional terms, stage 1 may be equated with the Holocene, stages 2-4 with the 'Last Glacial', and stage 5 with the 'Last Interglacial', though some authorities would prefer to restrict the Last Interglacial to sub-stage 5e, the only part of stage 5 that compared in overall warmth with the Holocene. In so far as it is possible below, the oxygen-isotope stage numbers are used in preference to the terms 'Last Interglacial' and 'Last Glacial', since the stages more fully reflect the true complexity of Upper Pleistocene and Holocene climatic change, particularly in the latitudes of southern Africa (roughly 10°S to 35°S).

'Large mammal' has been defined very loosely to include all mammalian species in which adults weigh at least 0.7-0.9 kg. The principal creatures excluded by this definition are bats, insectivores (except hedgehogs), and rodents (except primarily springhare, cane rats, the largest of the mole rats, and, of course, porcupines). The rationale for excluding 'small mammals' is that this paper is mainly concerned with mammalian remains as reflections of past human ecology, and it seems unlikely that people have ever systematically exploited mammals weighing less than 0.7-0.9 kg. Circumstantially, this proposition is supported by the fact that where small mammal remains have been found in large quantities in southern African sites (for example, at Redcliff Cave, Wonderwerk Cave, Die Kelders Cave 1, Byneskranskop Cave 1, Boomplaas Cave A, and Nelson Bay Cave), they are clearly concentrated in layers where artefacts and bones of large mammals are rare. This suggests that the small mammals were

TABLE 1
Upper Pleistocene oxygen-isotope stages defined in deep-sea cores
(based mainly on Shackleton & Opdyke (1973, 1976)).

<i>Approximate years B.P.</i>	<i>Oxygen-isotope stage</i>	<i>Inferred world climate</i>
0	1	very warm
12 000	2	very cold
32 000	3	cold with warmer oscillations
64 000	4	very cold
75 000	5a	warm
92 000	5b	cold
	5c	warm
109 000	5d	cold
	5e	very warm
128 000		

brought in mainly by predatory birds who occupied the sites when people were absent.

Of course, even though (or in part because) small mammal remains are generally not a product of human activity, they constitute a potentially valuable source of information about past environments, and their value in this regard is enhanced by the fact that it is often possible to obtain very large samples from relatively small excavations. Pertinent examples of palaeoenvironmentally oriented small mammal studies in southern Africa are those of Brain (1974a; Brain & Brain 1977) in the Namib Desert, and of Avery (1977 and in prep.) in the southern Cape Province. Brain has pointed out that fluctuations in the abundance of the principal species represented in the relatively simple microfaunas of the Namib can be used to monitor past changes in the amount of grass cover and of sand v. gravel in the vicinity of a site. In the more complex situation of the southern Cape, with a wider variety of well-represented microfaunal species, Avery is using sophisticated statistical procedures to detect relatively subtle changes in microfaunal communities, with the goal of checking and amplifying inferences on Upper Pleistocene and Holocene environmental change drawn from parallel studies of large mammal bones, palaeobotanical remains, and sediments.

MATERIALS AND PROBLEMS

The basic materials on which this paper is based are lists of large mammal species reported from Upper Pleistocene and Holocene sites in southern Africa. Both archaeological and non-archaeological sites have been surveyed, but among the archaeological ones, the focus is almost exclusively on sites occupied by Stone Age (v. Iron Age) people. People making stone artefacts were the only human occupants of southern Africa during the Pleistocene and most of the Holocene, and they persisted into the historic period over much of the sub-continent, especially in the Cape, Karoo-Namaqualian, and large parts of the Basutolian and Kalaharian Ecozones.

In the Zambesian and Transvaalian Zones, Stone Age people were progressively displaced by Iron Age agriculturists, beginning in the first centuries A.D. The Iron Age people were immigrants from further north, who subsequently also penetrated into those parts of the Basutolian and Kalaharian regions where their system of mixed farming was practicable. Iron Age faunas have been analysed from sites in Zambia by Fagan (1967; also Fagan *et al.* 1969), in Malawi by Voigt (1970, 1973, 1977), in Rhodesia by Brain (1974b) and Huffman (1974, 1975), in Botswana by Welbourne (1975), in the Transvaal by Voigt (1978) and Welbourne (1971, 1973), in Natal by Klein (as reported in Maggs & Michael 1976), and in the Orange Free State by Maggs (1975), but for the purposes of this paper the utility of the samples is limited, because most of them are small and they tend to be dominated by introduced domesticates (cattle, sheep and/or goats). However, the Iron Age lists have been scanned carefully for evidence they may contain on the distribution of indigenous mammals in relatively recent

times. For the most part, the lists support the distributional information that can be gleaned from early European travellers' reports or more recent historical sources, the most important exception being the presence of a possible gazelle in Malawi (Voigt 1973) and Natal (Klein unpub. in regard to the bovid listed as '*incertae sedis*' in Maggs & Michael 1976).

The non-archaeological and Stone Age sites which have provided the faunal lists on which this paper is based are listed in Tables 2-7. Since there are many sites and many of them are multilevel, it was not practical to reproduce the actual faunal lists here, but the overwhelming majority of them have been or soon will be published in sources listed in the tables.

In analysing the lists for palaeoenvironmental and palaeoecological information, the writer encountered two basic kinds of problems—ones that involved dating and ones that involved sample size and description. With regard to dating, the writer's major goal in most instances was to correlate a fauna with the appropriate oxygen-isotope stage as an important prerequisite to gauging its palaeoenvironmental implications. The isotope stage assignments on which the writer settled are presented in Tables 2-7, but even a rapid reading of the tables will show that in many instances no precise stage assignment was possible. The most secure stage (or substage) assignments are based on radiocarbon dates or on dates inferred from associated artefact assemblages whose radiocarbon ages are fairly well established. In particular, even where accompanying radiocarbon determinations were absent, the writer assumed that any southern African artefact assemblage that contained potsherds postdates 2 000 B.P. (that is, belongs to 'isotope stage 1, late'), that all assemblages which are readily assignable to the Wilton Industrial Complex of the Later Stone Age postdate 10 000 B.P. (belong to isotope stage 1), and that all assemblages which are classically Middle Stone Age antedate 30 000 B.P. (antedate isotope stage 2).

The principal dating difficulty stems from limitations inherent in the radiocarbon method, at least as practised by most laboratories, which make it relatively unreliable for dating sites that are older than 25 000 years, and of little or no utility for the precise placement of sites that are older than 40 000 years. For the moment, the most practical method of placing sites more precisely within the interval between 25 000-40 000 and 130 000 years is to correlate the sequence of climatic events they sometimes record with the general sequence of Upper Pleistocene climatic stages presented in Table 1. There are many sites to which such a dating procedure may never be applicable, and it has so far been applied only to a handful (especially to Border Cave (Butzer, Beaumont & Vogel 1978), Klasies River Mouth (Butzer 1978a), and various Cape coastal sites stratified in long aeolianite sequences (Butzer pers. comm.)). As a result, most southern African sites that are of earlier Upper Pleistocene age cannot at present be dated more precisely, even relative to one another, and this is a major obstacle to reconstructing patterns of environmental and cultural change. It is even possible that some supposedly earlier Upper Pleistocene localities actually date from the later part of the Middle Pleistocene (before 130 000 years ago), an

interval of time within which more precise dating is also extremely difficult. Neither artefacts nor fauna are very helpful in this context, since sites which have been dated on geological grounds to the late mid-Pleistocene (especially the lower levels of Border Cave (Butzer, Beaumont & Vogel 1978), the principal faunal occurrence at the Florisbad spring site (Butzer, Beaumont & Vogel 1978; Butzer pers. comm.), and Duinefontein 2 (Butzer, Beaumont & Vogel 1978; Butzer pers. comm.) contain artefact and/or faunal assemblages which are not easy to distinguish from those found at undoubted earlier Upper Pleistocene localities.

The problems with sample size and description are as serious as those with dating, though they are perhaps more easily avoidable in future research, since they generally stem from obvious deficiencies in excavation and analysis. The principal difficulty is that for many faunas, particularly those excavated prior to 1950, species lists have often been presented with little or no indication of absolute or relative species abundance, and, even where such indications are available, their utility is often vitiated by the fact that overall sample size is either not presented or is clearly very small. The absence of species frequency estimates and/or small sample size make it difficult, if not impossible, to determine in most instances if the differences between one faunal sample and another could be due simply to chance or if the differences are more likely to reflect differences in palaeoenvironments or in the agencies that accumulated the samples. It was, of course, to establish differences in palaeoenvironment or in agency of accumulation that the writer examined the faunal lists in the first place.

A further problem is that even where indices of species abundance have been presented and sample sizes are reasonable, the indices are not always strictly comparable. Because of limited experience, a lack of adequate comparative materials, or a shortage of time, some analysts have confined their identifications and counts only to the most diagnostic bones (usually teeth), while others have identified and counted a much wider range of skeletal parts. Further, in estimating species abundance, some investigators have presented the numbers of identifiable bones by which each species in a fauna is represented, while others have calculated the minimum numbers of individuals from which the bones are derived.

Even minimum individual counts are not necessarily comparable among sites because of differences in the kinds of provenience units to which counts have been attached or possible differences in the way in which the counts were calculated. At many sites, the provenience units are arbitrary spits that do not necessarily represent discrete occupations, and the minimum individual counts for any spit may well include individual animals that are also represented by bones in adjacent spits. In such a case, the counts may well be 'biased' versus counts from another site where the provenience units are natural layers that represent discrete occupations in which bones from the same individuals are very unlikely to occur. As an example of how methods of calculation may affect minimum individual counts, some investigators sort paired elements into lefts

and rights and take the minimum number of individuals represented by the element to be the higher number, left or right. Others simply divide the total number for the element by two. This and other differences in method of calculation are particularly likely to affect results in samples that are relatively small, as most southern African ones are.

Problems of sample size and description are more acute for sites in some areas than in others, and the best, most complete information, expressed in terms that make it possible to compare samples fairly rigorously, is available for the Cape Ecozone. The Cape Zone is also relatively rich in sites that are reasonably well dated, including several that sample the same time intervals, so that inferences about environmental or cultural change may be based on patterns which have been established at several localities. In other ecozones, the overall quality of the data is generally less satisfactory, and the palaeoenvironmental and palaeoecological inferences they allow are consequently more limited.

MAMMALIAN EVIDENCE FOR ENVIRONMENTAL CHANGE

In most cases, it is impossible to assume that the relative abundance of the mammalian species in a fossil assemblage reflects their relative abundance in the live community from which they were derived. By and large, it is far more reasonable to assume that their relative frequencies were altered in the process of bone accumulation (site formation), and generally speaking, the extent of alteration is impossible to determine. This makes it difficult to use most fossil faunas for the detailed reconstruction of an environment at any particular point in time.

On the other hand, there are instances of faunal samples that were accumulated by essentially the same agency (for example, Middle Stone Age people), whose effect in altering or 'biasing' species frequencies was probably more or less the same for all the samples. Differences in species frequencies between samples are then most likely to reflect a difference between the palaeoenvironments from which the samples were derived, and the nature of the environmental difference may be reasonably clear, even if the exact nature of the separate environments is not. More concretely, it may be possible to say, for example, that one environment contained more grazing animals than another, even if it is not possible to say precisely how many grazers were present in either environment.

And even if species frequencies in fossil faunas are not directly comparable to ones in living faunas, sometimes fossil faunas contain species which were never observed in the region of a site and which seem inappropriate to the region, given the known habitat preferences of the species elsewhere. In such instances, the mere presence of a species may be indicative of past environmental difference or change.

The purpose in this section is to present and interpret the available evidence for environmental change during the Upper Pleistocene and Holocene of southern Africa, as it is reflected in former large mammal distributions and in

changes through time in large mammal species frequencies. In so far as it is possible, an attempt has also been made here to determine the extent of congruency between environmental change reflected in large mammal faunas and change that has been established from other lines of evidence or that was perhaps predictable, given the placement of faunas in different global climatic (oxygen-isotope) stages.

The discussion will proceed ecozone by ecozone, starting with the most northern and ending with the most southern. For obvious reasons, the opening descriptions of the ecozones will emphasize the larger mammals they contain, particularly the species of bovids, equids, and suids. These species are the most common large mammals in the fossil faunas and also the ones whose past distributions or frequencies seem to have altered most dramatically. Least useful from a palaeoenvironmental point of view are the carnivores, both because they tend to be relatively rare in the fossil faunas and because most species, particularly the larger ones, are much less tied to particular habitats than the herbivores they prey on. They are therefore palaeoenvironmentally much less informative.

THE ZAMBESIAN ECOZONE

The Zambesian Zone is approximately coincident with the 'miombo woodlands', a vast stretch of wooded grassland extending more than 2 500 km from west to east and 1 200–2 000 km from north to south. In modern political terms, the Zambesian Zone comprises southern Tanzania, southern Zaire, most of Angola, Zambia, Malawi, northern Mozambique, and northern Zimbabwe Rhodesia.

Rainfall throughout the Zambesian region averages more than 500 mm/a, but it is almost entirely restricted to the summer months (December to May). On relatively well-drained ridges, hills, or interfluvies, the vegetation tends to consist of tall grass interspersed with deciduous trees (especially *Brachystegia* and *Julbernardia*) that lose their leaves in the dry season. In river valleys and along drainage lines (called dambos), trees, consisting mainly of acacias, are less common, and tall grasses predominate. Along the margins of river valleys, and especially in the southernmost part of the Zambesian Zone, the predominant tree in the savanna tends to be mopane (*Colophospermum mopane*). In typical miombo woodland (dominated by *Brachystegia* and *Julbernardia*), the grasses are of the 'sour' type that lose most of their nutritive value in the dry season. However, in mopane woodland, 'sweet' grasses that maintain their palatability throughout the year are more common, and as a consequence, mopane country tends to maintain a higher biomass of large grazing animals. It is only on the floodplains of the large rivers, however, that the Zambesian Zone supports numbers of large grazers to rival the numbers that occur or occurred on east and South African grasslands (in the Eastern and Basutolian regions of Figure 1).

Although the number of large mammals per unit area was generally less in the Zambesian Zone than in some others, the opportunities that it offers both browsers and grazers have led to unrivalled species diversity. In terms of biomass,

browsers were probably secondary overall, but at least locally, bushpig, bushbuck, Sharpe's grysbok, greater kudu, and grey duiker were (and in places still are) numerous in areas where browse and good cover are readily available. The principal grazers were Burchell's zebra, Lichtenstein's hartebeest, tsessebe, blue wildebeest, and warthog, occurring both in open woodland and in more open dambo areas. They shared the open woodland with sable antelope, roan antelope, and impala, which also tended to frequent more closed woodland. Southern reedbuck, waterbuck, puku, sitatunga, and especially lechwe and buffalo occurred on floodplains or floodplain margins. Eland, giraffe, elephant, and black rhinoceros occurred more or less throughout. White rhinoceros were locally common, and hippopotamus were present in all the large rivers. Among the smaller mammals, vervet monkey, baboon, hyraxes, hares, porcupine, cane rat, and springhare were all common, as were a wide range of carnivores, including all the top predators found elsewhere in Africa.

The pattern of Upper Pleistocene and Holocene environmental change in the Zambesian Zone is far from being established. The best available palynological and geomorphic data probably come from the Lunda area of north-eastern Angola (Clark 1963) and Kalambo Falls in north-eastern Zambia (Clark 1969) (also summaries of both areas in Butzer 1971a: 341-345). It is now clear that major parts of both sequences which were formerly assigned to the earlier Upper Pleistocene in fact date from the Middle Pleistocene, and also that there are problems with the precise chronological placement of parts of the sequences which are Upper Pleistocene in age. But the Lunda and Kalambo data still show that the later Pleistocene locally witnessed a succession of cooler and warmer phases, as well as a succession of wetter and drier ones. During the cooler periods, average yearly temperatures may have been as much as 3-5°C below what they are today. The major cool episodes probably correspond to the world-wide periods of colder climate reflected in deep-sea cores, but there was not necessarily correspondence between cooler periods and wetter ones. In fact, it is even possible that as it became wetter in one part of the Zambesian Zone, it became drier in another. It is now clear that Upper Pleistocene and Holocene periods of greater precipitation to the south-west of the Zambesian Zone (in the Kalaharian one) were often contemporaneous with drier ones to the north-east (in the Eastern one) (Butzer 1978b), and the situation in various parts of the Zambesian Zone must be investigated empirically before any generalizations may be made.

The Upper Pleistocene and Holocene sites in the Zambesian Zone that have provided remains of large mammals are listed in Table 2, along with the probable or suggested correlation of the sites (or of levels within them) with various oxygen-isotope stages. It is clear that faunal remains are available from sites correlated with several different stages, though precise stage placement is problematic in several instances (see Table 2 and below).

As a group, regardless of age, isotopic stage placement, or cultural associations, the various Zambesian sites tend to be dominated by large grazing

TABLE 2

Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Zambesian Ecozone.

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
<i>Isotope Stage 1, late (c. 5 000-0 B.P.)</i>			
Fingira Rock Shelter	Sandelowsky & Robinson (1968)	J. E. Mawby	LSA
Chencherere Rock Shelter II	Clark (1973)	D. Crader (n.d.)	LSA
Thandwe Rock Shelter	Phillipson (1976)	J. Harris	LSA
Kalemba Rock Shelter (levels 0-S)	Phillipson (1976)	J. Harris	LSA
Makwe Rock Shelter	Phillipson (1976)	B. M. Fagan & D. Davis	LSA, Iron Age
Leopard's Hill Cave (spits 1-8)	Miller (1969, 1971)	R. G. Klein	LSA
Gwisho Hot Springs B, C	Fagan & Van Noten (1971)	B. M. Fagan	LSA
Gwisho Hot Springs A	Gabel (1965)	L. H. Wells	LSA
<i>Isotope Stage 1, early (c. 12 000-5 000 B.P.)</i>			
Leopard's Hill Cave (spits 9-16)	Miller (1969, 1971)	R. G. Klein	LSA
<i>Isotope Stage 1, undifferentiated (c. 12 000-0 B.P.)</i>			
Nachikufu Cave	Clark (1950); Miller (1969, 1971)	H. B. S. Cooke (1950)	LSA
Mumbwa Caves (LSA levels)	Clark (1942)	R. Broom; H. B. S. Cooke (1950)	LSA
Inyanga (LSA caves)	Summers (1958)	H. B. S. Cooke (1958)	LSA
<i>Isotope Stage 2 (c. 32 000-12 000 B.P.)</i>			
Kalemba Rock Shelter (levels L-N)	Phillipson (1976)	J. Harris	LSA
Leopard's Hill Cave (spits 17-40)	Miller (1969, 1971)	R. G. Klein	LSA
Redcliff Cave ('Tshangula' levels)	Brain (1969a); Brain & Cooke (1967); C. K. Cooke (1978)	R. G. Klein (1978a)	LSA
<i>Isotope Stage 3 (c. 60 000-32 000 B.P.)</i>			
Redcliff Cave ('Later Bambata' levels)	Brain (1969a); Brain & Cooke (1967); C. K. Cooke (1978)	R. G. Klein (1978a)	MSA
<i>Isotope Stage 4 (c. 75 000-64 000 B.P.)</i>			
Redcliff Cave ('Earlier Bambata' levels)	Brain (1969a); Brain & Cooke (1967); C. K. Cooke (1978)	R. G. Klein (1978a)	MSA
<i>Isotope Stages 3, 4 and/or 5, undifferentiated</i>			
Kalemba Rock Shelter (levels G-K)	(c. 128 000-32 000 B.P.) Phillipson (1976)	J. Harris	MSA
Broken Hill (in part)	Clark <i>et al.</i> (1950)	Hopwood (1928); H. B. S. Cooke (1950); Leakey (1959)	MSA
Mumbwa Caves (MSA levels)	Clark (1942)	H. B. S. Cooke (1950)	MSA
Twin Rivers Kopje	Clark (1971)	H. B. S. Cooke	MSA

ungulates, particularly Burchell's zebra, warthog, and alcelaphine antelopes (blue wildebeest, hartebeest, and bastard hartebeest). These are the creatures which were predominant in most parts of the Zambesian Zone historically, suggesting definite limits to overall Pleistocene and Holocene environmental change, particularly as compared to the Cape Zone (discussed below) in which historically abundant mammals disappeared or became very rare on several occasions during the same interval.

Where there is deviation from the general pattern of dominance by zebra, warthog, and alcelaphines, it is toward an emphasis on other large grazing ungulates whose local abundance was predictable from the location and dating of a site. Thus, lechwe and buffalo are especially well represented at the late mid-Holocene ('isotope stage 1, late') spring sites at Gwisho, located on the margin of the Kafue floodplain on which these creatures were quite common historically (large herds of lechwe still occur near by). Zebra, warthog, blue wildebeest, and impala are also well represented in the Gwisho sites, presumably reflecting their prominence in the typical miombo woodland that flanks the Kafue floodplain at Gwisho. The long-term persistence of adjoining Kafue floodplain and miombo woodland habitats is clearly suggested by the much earlier (Middle Stone Age) fauna from Twin Rivers Kopje, which, like the Gwisho sites, is located on the margin of the Kafue floodplain, and which has also provided a fauna in which lechwe, wildebeest, and zebra are abundant, although precise numerical estimates are not available.

A further site in which creatures favouring near-water situations are very common is Kalembe Rock Shelter which has provided a relatively large number of bushpig and waterbuck remains. It is not clear that these creatures (at least waterbuck) were so abundant near Kalembe historically, and since their remains come principally from layers that probably belong in isotope stage 3 or 4, they may reflect once moister conditions near by.

The best evidence for environmental change in the Zambesian Zone, as reflected in mammalian fauna, comes from Redcliff Cave, where three species are present which did not occur in the Zambesian region in historic times, and which are so far unknown in any fauna clearly postdating isotope stage 2. These species are the blesbok, the common springbok, and the mountain reedbuck.

In an earlier publication on the Redcliff fauna, the writer suggested that the 'Tshangula' industry at the site was a late Middle Stone Age manifestation, similar perhaps to the Howieson's Poort variant of the Middle Stone Age further south (Klein 1978a). However, with the appearance now of a more complete report on the artefacts (C. K. Cooke 1978), the writer believes the 'Tshangula' industry is more likely to be an early Later Stone Age variant, dating to between 30 000 and 20 000 years B.P., as is in fact suggested by the single available radiocarbon date. This would place the 'Tshangula' industry and associated fauna in isotope stage 2.

The underlying Bambata levels, which are undoubtedly Middle Stone Age, are clearly beyond the range of radiocarbon dating, and their placement in one

or another isotope stage is not straightforward. However, Brain's (1969a) analysis of the Redcliff sediments is helpful in this regard. This shows that CaCO_3 concentration is relatively low and the matrix is relatively coarse in the earlier Bambata and especially in the Tshangula levels, perhaps reflecting stronger water flushing of the deposits, in turn reflecting moister climate. During accumulation of the intervening later Bambata levels, with a higher CaCO_3 content and finer matrix, conditions may have been generally drier.

If the Tshangula horizons are properly placed in isotope stage 2 and this was a relatively moist time near Redcliff, it seems most reasonable to place the earlier Bambata horizons, indicating comparable moistness, in the next oldest isotope stage that was generally comparable to '2' world-wide. This would be '4' (= early 'Last Glacial'). The intervening later Bambata levels, with their sedimentologic evidence for relative dryness, would then date from stage 3, during which world climates were generally less different from present ones than during stages 2 and 4. It is interesting in this context that the three 'exotic' species found at Redcliff are significantly more common in the Tshangula and earlier Bambata levels than in the later Bambata ones, suggesting that these species were locally most abundant during relatively moist intervals. All three presumably extended their ranges to Redcliff from regions much further south where they were common historically. Range extension Equatorwards (presumably as a result of vegetational change) might itself be taken as evidence for cooler conditions, moister conditions, or both.

The presence of common springbok in the Zambesian Zone is confirmed for stage 2 at Leopard's Hill Cave, where both radiocarbon dates and well-described associated (early Later Stone Age) artefacts leave no doubt about stage placement, although the overall Leopard's Hill faunal sample is too small for detailed palaeoenvironmental interpretation. There is no evidence that springbok survived into stage 1 (the Holocene) in the Zambesian region, but during this interval, a close east African relative of the springbok, the Thomson's gazelle, apparently penetrated the Zambesian Zone at least as far south as Kalembe Rock Shelter and perhaps also into Malawi, where a possible gazelle has been recorded in Iron Age sites (Voigt 1973) and in the broadly contemporaneous Later Stone Age deposits of Chencherere Rock Shelter II (Crader n.d.). In fact, the 'tommie' may have extended through the eastern portion of the Zambesian Zone into the Transvaalian one, if the writer's tentative identification of material from the Iron Age site of Ntshekane in the Tugela Basin of Natal is correct (Maggs & Michael 1976). Why the species did not occur in the Zambesian and Transvaalian Zones historically is not clear, but perhaps its absence is related in some way to the introduction and proliferation of domestic stock in Iron Age times.

THE TRANSVAALIAN ECOZONE

On the southern margin of the Zambesian Zone, mopane woodland tends to give way to shrubby acacia steppe or bushveld in a semi-arid setting. This

semi-arid country, running more or less across the continent, constitutes the Transvaalian Ecozone. As in the Zambesian Zone, rainfall is restricted almost entirely to summer, but the average is generally less than 500 mm/a, and there are great differences in total amount from year to year.

Of all the ecozones considered here, the Transvaalian one is the least satisfactory as a unit. It might well be better to consider it as three zones: (i) a western one, comprising the northern Transvaal, southern Zimbabwe Rhodesia, northern Botswana, northern South West Africa, and southern Angola; (ii) an eastern one, comprising the eastern Transvaal, adjacent south-western Mozambique, and eastern Swaziland; and (iii) a narrow southern extension comprising the Natal and south-eastern Cape coastal strips and their immediate hinterlands as far south-west as Port Elizabeth.

The western portion of the Transvaalian Zone, from the northern Transvaal westwards, is the driest part. The vegetation is typically grassland with interspersed shrubby trees, among which acacias are often most prominent. In a sense, the area is not so much a distinct ecozone as a transitional region between the Zambesian Zone to the north and the Kalaharian one to the south. Grazers (including blue wildebeest, Cape hartebeest, tsessebe, Cape buffalo, springbok, gemsbok, Burchell's zebra, and warthog) are most common, but browsers (greater kudu, bushbuck, giraffe, black rhinoceros *et al.*) and mixed feeders (eland and impala) are also prominent. Some of the large grazers incorporate parts of the Kalaharian Zone in their seasonal movements, and the transition to the Kalaharian region is clearly indicated by the presence of both gemsbok and springbok.

The eastern portion of the Transvaalian Zone, known in South Africa as the 'eastern Lowveld', is moister than the western. Bush and tree cover is much denser, and the term 'bushveld' is clearly appropriate. The overall variety of large mammal species is basically the same as to the west, but browsers and mixed feeders are more prominent numerically, as are grazers that prefer more wooded country (roan antelope, sable antelope, and buffalo). Springbok and gemsbok are absent.

The southern extension of the zone is covered by subtropical thornbush and scrub-forest in a subhumid rather than semi-arid setting. In the north, the fauna is very similar to that of the eastern Lowveld. Further to the south, beyond Zululand (KwaZulu), many of the Lowveld species drop out, and the fauna becomes essentially indistinguishable from that of the adjacent part of the Cape Ecozone.

Geomorphic evidence of former very large lakes in the Makarikari and Makgadikgadi Depressions (Street & Grove 1976; Grey & Cooke 1977), as well as interstratified evaporites and aeolian sands in a cave in the Kwihaba Hills of northern Botswana (Grey & Cooke 1977) demonstrate alternation between wetter and drier periods during the Upper Pleistocene and Holocene in the western part of the Transvaalian Zone. Data presented by Heine (1978) suggest that conditions were particularly wet 30 000 to 18 000 and again 11 000 years

ago, with arid conditions in between. If this is correct, then long-term precipitation trends in the western part of the Transvaalian Zone may have been out of phase with those immediately to the south in the Kalaharian Zone, where much of the interval between 18 000 and 11 000 B.P. appears to have been very wet (see Heine 1978 and below).

Levels of *éboulis secs* formed by frost weathering in Bushman Rock Shelter and Border Cave in the eastern part of the Transvaalian Zone (Butzer, Beaumont & Vogel 1978) document the intervals of much reduced Upper Pleistocene temperatures apparent in the deep-sea record. The sedimentary fills are not so informative about past precipitation changes, but it appears that there was no one-to-one correspondence between cooler and wetter periods. Sedimentation rates extrapolated from the radiocarbon-dated portion of the Border Cave sequence provide a basis for correlating the temperature fluctuations it records with ones established in the global marine record. The extent of temperature depression involved has not been established, but to the north, at Wolkberg Cave in the north-central Transvaal, the oxygen-isotope ratios of Upper Pleistocene cave carbonates have been used to suggest very tentatively that average temperatures during cold episodes were as much as 8.5–9°C below present ones (Talma *et al.* 1974).

Pollen recovered from peat deposits at Wonderkrater near Naboomspruit in the central Transvaal, indicates that, during at least some cooler phases, Transvaalian bushveld was replaced by open grassveld (Scott & Vogel 1978). It was presumably this kind of vegetational change which encouraged the spread of springbok and blesbok to the Cave of Hearths and Kalkbank, as discussed below.

The Upper Pleistocene and Holocene sites in the Transvaalian Zone that have provided remains of large mammals are listed in Table 3, along with the probable or suggested correlation of sites (or levels within them) with various oxygen-isotope stages. The Transvaalian Zone is second only to the Cape Zone in the number of sites correlated with various stages, but the available faunal samples are mainly small, incompletely described, or both.

The most dramatic changes through time in large mammal species frequencies have been recorded at Melkhoutboom Cave, located at the extreme south-western margin of the Transvaalian Zone, in an area that is transitional to the Cape Zone. Historically, the vegetation near Melkhoutboom was dominated by forest, closed bush, and sclerophyllous scrub, and the most common large mammals were various browsing ungulates—notably bushbuck, kudu, blue duiker, grysbok, and bushpig. The only prominent grazer was the Cape buffalo, which, in spite of its dietary preferences, is known to be very much at home in closed, bushy environmental settings.

The deposits at Melkhoutboom have provided a semi-continuous series of large mammal assemblages dating from approximately 15 400 to 2 000 years ago. The principal species in deposits dated to younger than 7 600 B.P. are the historically prominent browsers and the buffalo. However, in deposits older than

7 600 years, and particularly in ones older than 10 500 years, the browsers and buffalo are rare or absent, and the fauna is dominated by alcelaphine antelopes (black wildebeest, Cape hartebeest, blesbok/bontebok) and equid (either mountain zebra or quagga or both). This assemblage is more reminiscent of the fauna of the Basutolian Zone to the north than of the Transvaalian one in which Melkhoutboom is presently located. More generally, the pre-10 000 B.P. fauna from Melkhoutboom clearly suggests that the environs of the site were grassier in the terminal Pleistocene (late stage 2) than during most of the Holocene (stage 1). The same sort of vegetational change—from grassier to bushier or scrubbier—is reflected in faunal change within late Pleistocene to Holocene sequences at several sites in the near-by Cape Zone, as discussed below. The fact that the faunal change at Melkhoutboom and in the Cape Zone sites is so clear-cut probably reflects their position near the southern margin of the continent where Upper Pleistocene and Holocene environmental changes were perhaps more dramatic than in many areas nearer the Equator.

The basal levels at both Wilton and Uniondale, located not far east of Melkhoutboom, also perhaps date from a time (very early Holocene or terminal Pleistocene) when large grazers were relatively common near-by, but the faunal samples are far too small to document this. At both sites, the bulk of the fauna comes from mid to late Holocene levels, and the principal species represented are the same ones that dominate the contemporaneous deposits at Melkhoutboom—bushpig, bushbuck, duiker, grysbok or steenbok, and Cape buffalo.

An earlier Upper Pleistocene interval broadly comparable to the terminal Pleistocene at Melkhoutboom may be reflected in the fauna from Aloes, also in the transitional area between the Transvaalian and Cape Zones. Land-snail shells associated with the bones at Aloes yielded a radiocarbon age of greater than 37 000 years. The relatively large sample has provided no identifiable bones of browsers, though large grazers (quagga, 'giant Cape horse', wildebeest, common springbok, and warthog) are well represented.

In the heartland of the Transvaalian Zone, far to the north, the available evidence suggests that faunal change related to more general environmental change was more subtle than at Melkhoutboom, but such change did occur. This is particularly clear at Border Cave, which has provided analysable faunal remains from deposits correlated with deep-sea isotope stages 5d through 3. Using the number of squares in which bones of a species occur as an index of its abundance in each Border Cave level, the writer has been able to show that levels in which bushpig, Cape buffalo, tragelaphine antelopes (kudu, nyala, bushbuck, and eland), and impala are relatively common, alternate with levels in which warthog, Burchell's zebra, and alcelaphine antelopes are more prominent.

Warthog, zebra, and alcelaphines were probably more common near by in historic times, and the writer has suggested that levels in which bushpig and buffalo are relatively abundant reflect Upper Pleistocene intervals in which the vegetation contained more bush than in recent times. This conclusion is supported by analysis of the sediments (Butzer, Beaumont & Vogel 1978),

TABLE 3
Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Transvaalian Ecozone.

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
<i>Isotope Stage 1, late (c. 5 000-0 B.P.)</i>			
Onink	Beaumont (pers. comm.)	R. G. Klein	LSA
Embabeni	Beaumont (pers. comm.)	R. G. Klein	LSA
Shongweni (upper occupation)	Davies (1975)	R. G. Klein & P. L. Carter	LSA
Fairview	Robertshaw (pers. comm.)	R. G. Klein	LSA
Ann Shaw (MAJ)	Derricourt (1977)	R. G. Welbourne	LSA
Wilton (levels 1-3F)	J. Deacon (1972)	C. K. Brain	LSA
Melkhoutboom (levels CAF, OMB)	H. J. Deacon (1976)	R. G. Klein	LSA
<i>Isotope Stage 1, early (c. 12 000-5 000 B.P.)</i>			
Bushman Rock Shelter	Louw (1969); Eloff (1969); Plug (unpub.)	C. K. Brain (1969b); I. Plug	LSA
Heuningsneskrans (layers 3, 2)	Vogel & Marais (1971); Beaumont (pers. comm.)	J. Kitching	LSA
Mlaula	Beaumont (pers. comm.)	R. G. Klein	LSA
Wilton (levels 3G-4)	J. Deacon (1972)	C. K. Brain	LSA
Melkhoutboom (levels MB-RF)	H. J. Deacon (1976)	R. G. Klein	LSA
<i>Isotope Stage 1, undifferentiated (c. 12 000-0 B.P.)</i>			
Pomongwe (Pomongwan and Wilton levels)	C. K. Cooke (1963)	C. K. Brain as reported in Sampson (1974)	LSA
Uniondale	M. Brooker (pers. comm.)	R. G. Klein	LSA
<i>Isotope Stage 2 (c. 32 000-12 000 B.P.)</i>			
Heuningsneskrans (layer 1)	Vogel & Marais (1971); Beaumont (pers. comm.)	J. Kitching	LSA
Shongweni (lower occupation)	Davies (1975)	R. G. Klein & P. L. Carter	LSA
Melkhoutboom (level B)	H. J. Deacon (1976)	R. G. Klein	LSA
<i>Isotope Stage 3 (c. 64 000-32 000 B.P.)</i>			
Border Cave (1BS1r-2BS1rA)	Beaumont <i>et al.</i> (1978); Butzer, Beaumont & Vogel (1978)	R. G. Klein (1977)	LSA and MSA
<i>Isotope Stage 4 (c. 75 000-65 000 B.P.)</i>			
Border Cave (2 BS1rB, C)	Beaumont <i>et al.</i> (1978); Butzer, Beaumont & Vogel (1978)	R. G. Klein (1977)	MSA

(Cont.)

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
<i>Isotope Stages 3 and 4, undifferentiated (c. 75 000–32 000 B.P.)</i>			
Bushman Rock (later MSA levels)	Louw (1969); Eloff (1969); Plug (unpub.); Butzer (in prep.)	C. K. Brain (1969b); I. Plug	MSA
<i>Isotope Stage 5a</i>			
Border Cave (2WA, 3BSup)	Beaumont <i>et al.</i> (1978); Butzer, Beaumont & Vogel (1978)	R. G. Klein (1977)	MSA
<i>Isotope Stage 5b</i>			
Border Cave (3BS1r, 3WA)	Beaumont <i>et al.</i> (1978); Butzer, Beaumont & Vogel (1978)	R. G. Klein (1977)	MSA
<i>Isotope Stage 5d</i>			
Border Cave (1GBSup, 1r)	Beaumont <i>et al.</i> (1978); Butzer, Beaumont & Vogel (1978)	R. G. Klein (1977)	MSA
<i>Isotope Stages 3, 4, and/or 5, undifferentiated (c. 128 000–32 000 B.P.)</i>			
Pomongwe (MSA layers)	C. K. Cooke (1963)	C. K. Brain as reported in Sampson (1974)	MSA
Chelmer	Bond & Summers (1951)	H. B. S. Cooke & L. H. Wells (1951); H. B. S. Cooke (1963)	none
Bulawayo Waterworks Kalkbank	Zealley (1916) Mason (1962, 1967); Mason <i>et al.</i> (1958)	A. E. V. Zealley & S. Haughton H. B. S. Cooke (1962); R. G. Welbourne (1971)	none MSA
Cave of Hearths Aloes	Mason (1962) Gess (1969)	H. B. S. Cooke (1962) L. H. Wells (1970a)	MSA none

which establishes a general correspondence between apparently colder episodes, as reflected in sediments, and 'bushier' fauna. Unfortunately, the faunal samples from various levels are too small for a truly detailed study of the relationship between changes in sediment parameters and species frequencies.

Yet further north, environments different at one or more times during the Upper Pleistocene from modern ones are probably implied by the presence of common springbok and of blesbok/bontebok at the Cave of Hearths and especially at Kalkbank. Both sites are located north of the areas in which these species were distributed in historic times (Kettlitz 1962). In the vicinity of both sites, the impala apparently fills the niche occupied by the springbok elsewhere, yet in the fossil fauna from Kalkbank, for which species frequency estimates are available, springbok is actually more common than impala. The occurrence of springbok and of bontebok/blesbok in earlier Upper Pleistocene contexts at the Cave of Hearths and Kalkbank was perhaps to be expected in view of their presence in broadly contemporaneous deposits at Redcliff yet further north, and probably reflects the same vegetational change (less bush, more grass) as at Redcliff.

THE KALAHARIAN ECOZONE

This ecozone corresponds broadly to that part of the southern African interior plateau that is often known as the Kalahari desert, though it is not really a desert in either climatic or vegetational terms. With regard to modern political units, the Kalaharian Zone covers eastern South West Africa, the western two-thirds of Botswana, and a large portion of the adjacent (northern) Cape Province of South Africa.

Rainfall in the Kalaharian Zone is erratic and comes almost entirely in summer. The average decreases from roughly 500 mm/a in the north-west to as little as 200 mm in the south-west. Highly porous, sandy soils soak up rainfall rapidly, so that surface water is relatively rare, even in areas where the average rainfall is fairly high. Vegetation cover is highly variable, from relatively luxuriant acacia savanna with an important grass component in the better watered parts (particularly in the north) to sparse shrub acacia savanna and bushveld in the more arid parts (particularly in the south).

At least historically, the grass cover over much of the Kalaharian region was sufficient to support fair numbers of gregarious, migratory grazing ungulates, particularly ones which are capable of obtaining their moisture requirements largely from plants. Springbok and gemsbok were especially common, and blue wildebeest, hartebeest, Burchell's zebra, and warthog were at least locally abundant. Browsing animals, including especially giraffe and greater kudu, were generally less common. Among mixed feeders, eland and steenbok were widespread. Bushbuck (a browser), Cape buffalo and roan antelope (grazers), and impala (a mixed feeder) occurred in some areas of denser bush. Among non-ungulate herbivores, hare(s), springhare, porcupine, baboon, and rock hyrax were (and in some cases still are) widespread and abundant. The principal

carnivores preying on these creatures or scavenging on their carcasses were lion, leopard, cheetah, brown hyena, spotted hyena, Cape hunting dog, and jackals.

Upper Pleistocene and Holocene environmental change within the Kalaharian Zone has been best documented by geomorphic research at its south-eastern margin, particularly along the Gaap Escarpment in the northern Cape Province (Butzer, Stuckenrath *et al.* 1978). Alternation of subhumid and semi-arid climatic phases is apparent in the Gaap sequence, with the earliest radiocarbon-dated subhumid phase fixed between $\geq 21\,000$ and 14 000 years ago. Subsequent subhumid phases are dated between 9 700 and 6 500 B.P. and between 4 500 and 400 B.P. Long-term fluctuations in precipitation appear to be broadly in phase with those recorded in the Basutolian Zone to the east, but not necessarily with those in the Transvaalian Zone to the north (see above and Heine 1978).

Beds of cryoclastic rubble document several past episodes of relatively intense cold along the Gaap Escarpment and presumably throughout the Kalaharian Zone. The most recent very cold interval clearly coincided with deep-sea stage 2. The greatest cold appears to have preceded and followed the marked subhumid phase between $\geq 21\,000$ and 14 000 B.P., indicating that the relationship between past temperature and precipitation change was a complex one.

The Upper Pleistocene and Holocene sites in the Kalaharian Zone which have provided remains of large mammals are listed in Table 4, along with the probable correlation of the sites (or of levels within them) with various oxygen-isotope stages. Most of the sites are located on the south-eastern margin and date from the late Holocene. The late Holocene faunal samples are dominated by hare(s), springhare, rock hyrax, Burchell's zebra or quagga, warthog, black wildebeest and/or Cape hartebeest, springbok, and steenbok. The mountain reedbuck is also relatively common, reflecting the relatively rugged topography surrounding many of the sites. In no case is there any clear suggestion of an environmental setting that differed significantly from the historic one.

With the important exception of the fauna from Equus Cave, which has been sorted and identified, but not yet analysed, the faunas from Kalaharian sites of Pleistocene age are either small, poorly excavated, incompletely reported, or all three. Most of them are also very imprecisely dated. All this makes it difficult to assess their palaeoenvironmental significance. However, the occurrence of blesbok/bontebok at Black Earth Cave, Witkrans Cave, and especially at Gobabis far to the north-west of the species' historic range, suggests a vegetation cover in which perennial grasses may have played a greater role than they did historically in the Kalaharian region. The occurrence of vaalribbok at Black Earth Cave, Ochre Cave, and Boetsap may have broadly similar implications, depending upon how common it was in the deposits (the samples presently available for study are all highly selected and therefore not suitable for establishing species frequencies). The vaalribbok occurred near all the sites in historic times, but was not especially common. It has so far not been recorded in local

TABLE 4
Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Kalahari Ecozone.

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
<i>Isotope Stage 1, late (c. 5 000-0 B.P.)</i>			
Witkrans Cave ('Wilton' level)	Peabody (1954)	H. B. S. Cooke (n.d.)	LSA
Little Witkrans	Peabody (1954); Beaumont (pers. comm.)	H. B. S. Cooke (n.d.); R. G. Klein	LSA
Powhouse Cave	Peabody (1954); Humphreys (1978)	R. G. Klein (1979a)	LSA
Limerock 1, 2	Humphreys (in prep.)	R. G. Klein (1979a)	LSA
Dikbosch 1, 2	Humphreys (1974, and in prep.)	R. G. Klein (1979a)	LSA
Burchell's Shelter	Humphreys (1975)	R. G. Klein (1979a)	LSA
Doomfontein	Beaumont & Boshier (1974)	J. Kitching	LSA
Wonderwerk Cave ('later Smithfield')	Beaumont (pers. comm.); Butzer (pers. comm.)	unidentified	LSA
≠g1 (LSA level)	Brooks & Yellen (1979)	R. G. Welbourne	LSA
<i>Isotope Stage 1, early (c. 12 000-5 000 B.P.)</i>			
Wonderwerk Cave ('earlier Smithfield')	Malan & Cooke (1941); Malan & Wells (1943); Beaumont (pers. comm.); Butzer (pers. comm.)	H. B. S. Cooke & L. H. Wells	LSA
<i>Isotope Stage 1, undifferentiated (c. 12 000-0 B.P.)</i>			
Ochre Cave	Peabody (1954)	H. B. S. Cooke (unpub.)	LSA
<i>Isotope Stage 5 (c. 128 000-75 000 B.P.)</i>			
Witkrans Cave (MSA levels)	Peabody (1954); Clark (1971); Butzer, Stuckenrath <i>et al.</i> (1978)	H. B. S. Cooke (unpub.)	MSA
Equus Cave	Beaumont & Shackley (pers. comm.); Butzer, Stuckenrath <i>et al.</i> (1978)	R. G. Klein	none
Gobabis	Jacobson (1978a); Butzer (pers. comm.)	R. G. Klein	none
<i>Isotope Stages 3, 4 and/or 5, undifferentiated (c. 128 000-32 000 B.P.)</i>			
Black Earth Cave	Peabody (1954)	H. B. S. Cooke (unpub.); R. G. Klein	none
Boetsap	Peabody (1954)	H. B. S. Cooke (unpub.); R. G. Klein	none
Munro's Site (Oppermansdrif faunal locality)	Mason (1969)	R. G. Welbourne (1971)	none
≠g1 (MSA level)	Yellen (1971); Helgren (1978); Brooks & Yellen (1979)	R. G. Welbourne	MSA

late Holocene faunas (unless the fauna from Ochre Cave dates from this interval). It is a hillside grazer which is most at home in the Basutolian and Cape Zones, where its frequency in both live communities and archaeological sites tends to be highly correlated with and subequal to that of mountain reedbuck. Moister conditions may well be implied if it were as frequent as mountain reedbuck in a Kalaharian fossil fauna.

THE BASUTOLIAN ECOZONE

This zone comprises the Drakensberg Mountains and the high plateau country adjacent to them. In modern political terms, it covers the southern Transvaal, the western quarter of Swaziland, the highlands of western Natal, all of Lesotho, most of the Orange Free State, and a portion of the adjacent eastern Cape Province. The area is characterized by warm, relatively moist summers (average precipitation generally between 620 and 750 mm) and cold, dry winters. East of the Drakensberg, the historic vegetation of the Basutolian Zone was primarily open grassland with patches of temperate forest at the heads of river valleys and areas of acacia savanna at lower altitudes. West of the Drakensberg, in the area known in South Africa as the 'highveld', the vegetation was nearly pure grassveld with trees largely confined to the river valleys.

Historically, the fauna of the Basutolian region was dominated overwhelmingly by large, migratory, gregarious grazers, especially Burchell's zebra, the recently extinct quagga, black wildebeest, blesbok, and springbok. Their numbers may even have exceeded those of their counterparts in the east African grasslands, and it is probable that they were interdependent in a grazing succession similar to that recently observed in east Africa. They probably migrated with the seasons in search of good pasture, and it is likely the migrations took in the eastern part of the Karoo-Namaqualian Zone into which the Basutolian one merges imperceptibly.

In keeping with the open nature of the vegetation, browsers (greater kudu, bushbuck, etc.) and grazers favouring wooded country (roan, sable, Cape buffalo) were rare or absent in the Basutolian Zone. The impala was completely displaced by the springbok, but eland and steenbok, also mixed feeders, were widespread. Warthogs were numerous, but bushpigs were generally absent. Mountain reedbuck, vaalribbok, and to a lesser extent klipspringer were common in areas of high relief. Among smaller mammals, hares, springhare, and rock hyrax are still abundant in many places.

Pollen-analytical studies undertaken at Florisbad by Van Zinderen Bakker (1957) and at Aliwal North by Coetzee (1967), both located near the western margin of the Basutolian Zone, reveal that the local grassveld was replaced at various times in the later Pleistocene by semi-desert shrub of the Karoo-Namaqualian Zone. At Aliwal North, where the sequence is reliably dated between approximately 13 200 and 9 600 B.P., a replacement of grassveld by Karoo shrub (and the reverse) occurred three times, reflecting relatively rapid fluctuations between cooler/moister and warmer/drier conditions similar to the

kind of relatively rapid climatic fluctuations that are known to have characterized the contemporaneous terminal Pleistocene/Holocene transition in Europe.

At Florisbad, the pollen spectra are all much older and precise dating is a problem, though a grassveld phase indicating relatively moist conditions occurs in deposits that probably correlate with deep-sea isotope stage 2. Studies of alluvial cut-and-fill sequences in the Upper Orange drainage by Butzer (1971*b*) also indicate that stage 2 times were generally wet in the Basutolian Zone, as they were in the neighbouring Kalaharian one. Yet earlier wetter and drier phases are difficult to date, and it is clear that the ones reflected in pollen spectra at Florisbad are beyond the range of radiocarbon. The earliest part of the Florisbad sequence, in fact, probably dates from the later mid-Pleistocene.

The Upper Pleistocene and Holocene sites in the Basutolian Zone which have provided remains of large mammals are listed in Table 5, along with the probable correlation of the sites (or of levels within them) with various oxygen-isotope stages. Most of the sites are located near the western margin of the zone and either date very clearly from the late Holocene or are difficult to date precisely.

The late Holocene faunas are dominated by hare(s), rock hyrax, Burchell's zebra and/or quagga, black wildebeest, springbok, and steenbok, suggesting an environment broadly similar to the historic one. Faunas coming from sites located in more rugged topography are clearly marked by a higher frequency of mountain reedbuck and vaalribbok, as would be expected.

The pre-Holocene faunas are also dominated by large gregarious grazers, suggesting general limits to the extent of later Pleistocene environmental change. However, the presence of lechwe or waterbuck at Vlakkraal and Koffiefontein, of Cape buffalo at Koffiefontein and Driefontein, of impala at Koffiefontein, and of roan at Driefontein, may reflect moister conditions at one or more times during the earlier Upper Pleistocene. The lechwe is also present at Florisbad, but its stratigraphic provenience within the site is unknown. It may have come either from Upper Pleistocene levels, from levels that probably date to the late mid-Pleistocene, or from both. The same problems of provenience, reflecting relatively uncontrolled excavations, make it impossible to relate various elements in the Florisbad fauna to the palynological and geomorphic observations that have been made at the site, but the fauna is further interesting for the presence of hippopotamus, suggesting a time(s) when the pan next to the site may have contained a lake. The occurrence of water mongoose and clawless otter may reflect the same moist interval(s). Perhaps even more intriguing is the occurrence of giraffe, which must indicate that trees once grew near by, though the area was treeless historically, and Van Zinderen Bakker found virtually no arboreal pollen in any of the samples he examined from the site.

THE KAROO-NAMAQUALIAN ECOZONE

This zone has two major components: (i) the Namib Desert, a narrow strip up to 160 km wide along the Atlantic coast, extending from the mouth of the Orange River through South West Africa to beyond Mossamedes in Angola;

TABLE 5

Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Basutolian Ecozone.

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
<i>Isotope Stage 1, late (c. 5 000-0 B.P.)</i>			
Driel Shelter	Maggs (pers. comm.)	R. G. Klein	LSA
Moshebi's Shelter	Carter (1969, 1977); Carter & Vogel (1974)	P. L. Carter	LSA
Melikane	Carter (1977)	P. L. Carter	LSA
Sehonghong	Carter (1977); Carter & Vogel (1974)	P. L. Carter	LSA
Bellevue	Carter (1977)	P. L. Carter	LSA
Rose Cottage Cave	Malan (1952); Butzer (pers. comm.)	unidentified	LSA
Ventershoek	Sampson (1970)	R. G. Klein (1979a)	LSA
Holmsgrove	Sampson (1970)	unidentified	LSA
Zaayfontein	Sampson (1967a, 1970)	J. Kitching	LSA
Riversmead	Sampson & Sampson (1967)	R. G. Klein (1979a)	LSA
Glen Elliott Shelter	Sampson (1967b)	R. G. Klein (1979a)	LSA
Blydefontein	Sampson (1970)	R. G. Klein (1979a)	LSA
Tafelberg Hall	Hewitt (1931)	?	LSA
Highlands Shelter	H. J. Deacon (1976)	R. G. Klein	LSA
<i>Isotope Stage 2 (c. 32 000-12 000 B.P.)</i>			
Sehonghong	Carter (1977); Carter & Vogel (1974)	P. L. Carter	LSA
Florisbad (Peat III)	Dreyer (1938); Hoffman (1955); Meiring (1956); Butzer (1971b and pers. comm.)	H. B. S. Cooke & Wells; H. B. S. Cooke (1963)	?
<i>Isotope Stage 5 (c. 128 000-75 000 B.P.)</i>			
Florisbad (Peat II)	Dreyer (1938); Hoffman (1955); Meiring (1956); Butzer (1971b and pers. comm.)	H. B. S. Cooke & Wells; H. B. S. Cooke (1963)	?MSA
Vlakkraal	Wells <i>et al.</i> (1942); Butzer (1971b; and pers. comm.)	H. B. S. Cooke & Wells; H. B. S. Cooke (1963)	MSA
Koffiefontein	H. B. S. Cooke (1948); Butzer (1971b; and pers. comm.)	H. B. S. Cooke	?
<i>Isotope Stages 3, 4 and/or 5, undifferentiated (c. 128 000-32 000 B.P.)</i>			
Melikane	Carter (1977)	P. L. Carter	MSA
Sehonghong	Carter (1977); Carter & Vogel (1974)	P. L. Carter	MSA
Driefontein	Wells (1970b)	L. H. Wells; R. G. Klein (1974a)	?MSA

and (ii) the Karoo, a great plain stretching across the Cape Province from the Orange River on the north to the Cape Folded Mountains on the south.

The Namib is the most extreme desert in southern Africa. Average rainfall within it nowhere exceeds 130 mm/a, and there are many places where it is less than 25 mm. Vegetation is largely confined to the major river valleys, except after occasional rains when stands of annual grasses briefly appear. The southern part of the Namib (south of the Kuiseb River) is a dune sea, while the northern part consists primarily of gravel plains and barren, rocky hills. The principal large mammals in the desert proper are gemsbok and springbok, supplemented by rock hyrax, hares, steenbok, klipspringer, and mountain zebra in some hillier parts and on the dissected escarpment that separates the desert from the Kalaharian Zone to the east.

The Karoo is less arid than the Namib, with average rainfall varying between 130 and 400 mm/a, depending on the place. Over most of the Karoo, rain comes primarily in summer, but in the south-western parts, as much as half may come in winter. Typical Karoo vegetation is low scrub with much bare ground in between and a sparse scattering of grasses. Trees, consisting mainly of acacias, are confined to the river valleys. The density of grass increases towards the east, until the Karoo merges more or less imperceptibly with the grassveld of the Basutolian region. The most common large mammals in the Karoo were probably rock hyrax, hare(s), springbok, gemsbok, black wildebeest, steenbok, grey duiker, and quagga.

Hard evidence for Upper Pleistocene and Holocene environmental change in the Karoo-Namaqualian Zone is sparse and has been summarized by Coetzee (1978a). Geomorphic features pointing to once wetter conditions, even in the Namib, are relatively widespread, but the dates of the wetter periods remain unestablished.

The Upper Pleistocene and Holocene sites in the Karoo-Namaqualian Zone that have provided remains of large mammals are listed in Table 6, along with the probable correlation of the sites (or of levels within them) with various oxygen-isotope stages. The sites are divisible into two basic groups: to the north, a series of rock shelters in hilly areas adjacent to the Namib Desert, and to the south, Elands Bay Cave in a part of the Karoo that is transitional to the Cape Zone. Fossiliferous Upper Pleistocene or Holocene sites within the Karoo or Namib proper are virtually unknown so far, excepting some very recent coastal middens yielding mainly remains of pinnipeds (Jacobson & Klein unpub.; Thackeray 1975, 1979), Mirabib Rock Shelter, from which only the microfauna has been identified (Sandelowsky 1974, 1977; Brain & Brain 1977), and 'Namib 2', a locality just south of the Kuiseb recently discovered by Shackley (pers. comm.).

The hilly, rocky topography surrounding the sites located on the margins of the Namib is clearly reflected in their faunas, in which rock hyrax and klipspringer are very common. Hares, an equid that is probably mountain zebra, springbok, and steenbok are also relatively well represented. Although some

TABLE 6

Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Karoo-Namaqualian Ecozone.

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
<i>Isotope Stage 1, late (c. 5 000-0 B.P.)</i>			
Brandberg Sites (Lower Numas Cave, Orabes Shelter 4, Tirara Shelter, Girls' School Shelter)	Jacobson (1978b)	R. G. Klein	LSA
Fackelträger	Wendt (1972); Thackeray (1979)	C. K. Brain	LSA
Big Elephant Shelter	Wadley (1976, 1979)	R. G. Klein	LSA
Striped Giraffe Shelter	Wadley (1979)	I. Plug (1979)	LSA
Nos	Wendt (unpub.)	F. Thackeray (1979)	LSA
Namtib	Wendt (1972)	F. Thackeray (1975, 1979)	LSA
Tiras 5	Wendt (1972)	F. Thackeray (1975, 1979)	LSA
Haalenberg	Wendt (unpub.); Thackeray (1979)	R. G. Klein	LSA
Aar I and II	Wendt (1972)	F. Thackeray (1975, 1979)	LSA
Pockenbank (LSA)	Wendt (1972)	F. Thackeray (1975, 1979)	LSA
Apollo 11 ('Pottery LSA')	Wendt (1972)	F. Thackeray (1975, 1979)	LSA
Elands Bay Cave (levels 1-9)	Parkington (1972, 1976, 1978, n.d.)	R. G. Klein	LSA
<i>Isotope Stage 1, early (c. 12 000-5 000 B.P.)</i>			
Apollo 11 ('Wilton')	Wendt (1972, 1976)	F. Thackeray (1975, 1979)	LSA
Elands Bay Cave (levels 17-10)	Parkington (1972, 1976, 1978, n.d.)	R. G. Klein	LSA
<i>Isotope Stage 2 (c. 32 000-12 000 B.P.)</i>			
Apollo 11 ('Early LSA')	Wendt (1972, 1976)	F. Thackeray (1975, 1979)	LSA
Elands Bay Cave (levels 20-18)	Parkington (1972, 1976, 1978, n.d.)	R. G. Klein	LSA
<i>Isotope Stages 3 and/or 4, undifferentiated (c. 75 000-32 000 B.P.)</i>			
Apollo 11 ('Blade MSA')	Wendt (1972, 1976)	F. Thackeray (1975, 1979)	MSA
Pockenbank (MSA)	Wendt (1972)	F. Thackeray (1975, 1979)	MSA
<i>Isotope Stage 5 (c. 128 000-75 000 B.P.)</i>			
Apollo 11 ('Crescent MSA' and Older MSA)	Wendt (1972, 1976)	F. Thackeray (1975, 1979)	MSA

of the samples clearly date from Upper Pleistocene intervals in which climatic conditions were certainly different from modern ones, there is no faunal evidence for a significantly different past environment. The reason is perhaps small sample size more than a real lack of Upper Pleistocene faunal and environmental change.

Elands Bay Cave is located on the Atlantic coast, far south of the other sites, in an area that is transitional between the Karoo-Namaqualian and Cape Zones. The cave has provided relatively large faunal assemblages bracketed between roughly 17 000 B.P. and the historical present, though there is a major gap in the sequence from approximately 8 000 to 4 000 B.P. Large grazing ungulates are relatively more common in levels ante-dating 9 000 B.P., suggesting that grasses were relatively more important near by in the late Pleistocene than in the Holocene. The same kind of faunal change, probably also reflecting a reduced role for grasses in the Holocene, is even more apparent at sites located within the near by Cape Zone. An increase in the frequency of steenbok relative to grysbok in Elands Bay levels postdating 9 000 B.P. perhaps reflects subtle, but locally significant, changes in the nature of the non-grass component of the vegetation near the site.

Like coastal sites in the Cape Zone that contain a comparable late Pleistocene/Holocene sequence, Elands Bay further records the terminal Pleistocene/early Holocene rise in sea-level. During the period of much depressed sea-levels between 17 000 and 12 000 years ago, the coastline was always more than 10 km from the site, and remains of marine creatures are very rare in deposits dating from this interval. By 11 000 B.P., the coastline had probably moved to within 4 km of the site, and most kinds of edible marine creatures, prominently including the Cape fur seal, first appear in deposits of about this age. By 9 000 B.P. or so, the coast was in approximately its present position, and remains of marine species are superabundant in all the younger levels.

THE CAPE ECOZONE

By far the smallest of the ecozones considered here, this zone consists of the Cape Folded Mountains and the adjacent coastal plains. The mountains set it off from the Karoo-Namaqualian Zone to the north, and a spur of the mountains reaching the sea at Cape Hangklip separates the coastal plain into two usefully distinguished parts—the south-western Cape and the southern Cape. The south-western Cape has a typically Mediterranean climate, with wet, cool winters and hot, dry summers. The southern Cape is also marked by strong seasonal contrasts in temperatures, but rainfall tends to be more evenly distributed throughout the year, especially to the east.

The vegetation typical of much of the Cape Ecozone is known locally as fynbos and bears a broad resemblance to the macchia of the Mediterranean region. Typical fynbos plants are shrubs of various kinds with small, hard leaves that are capable of withstanding summer drought. The principal families are reeds (*Restionaceae*), heaths (*Ericaceae*), and proteas (*Proteaceae*). Irises

and orchids (*sensu lato* Iridaceae and Orchidaceae) are common, but grasses (Gramineae) are relatively rare. At least historically, the higher slopes of the mountains in the western part of the region bore forests of 'cedar' (*Widdringtonia*), while the lower mountain slopes and adjacent coastal plain in the south-eastern part of the zone, centred roughly on the town of Knysna, carried a mixed forest of yellowwood and evergreen broadleaf trees. Smaller stands of essentially the same kind of mixed forest occurred in relatively moist, sheltered microenvironments elsewhere in the Cape Zone as well.

Reflecting the nature of the vegetation, at least historically the fauna of the Cape Ecozone was dominated by browsing ungulates. In the southern Cape, the principal browsers were bushpig, bushbuck, blue duiker, grey duiker, and Cape grysbok. Among the grazers, only the Cape buffalo was common more or less throughout. Hartebeest was locally fairly numerous. Bontebok and blue antelope, though entirely restricted (endemic) to this region were rare, and the blue antelope became extinct about 1800 A.D. Roan antelope occurred in small numbers in the forests of the south-east. Eland and steenbok (mixed feeders) occurred more or less throughout, though the steenbok was probably completely replaced by the grysbok in areas of dense fynbos, bush, or forest. Vaalribbok and mountain reedbuck were common in suitably hilly locales, particularly in the flanking Cape Mountains, where they were joined by the mountain zebra. The most common non-ungulate herbivores were baboons, rock hyraxes, porcupines, and hares. On the west, a large endemic mole-rat (*Bathyergus suillus*) was also abundant in sandy, mainly coastal areas. Cape fur seal was common in coastal waters, and rookeries even occurred on the mainland.

The fauna of the south-western Cape was similar, but more impoverished, lacking bushpig, bushbuck, blue duiker, buffalo, mountain reedbuck, blue antelope, roan, bontebok, and other species found in the southern Cape. Grey duiker was relatively abundant and steenbok was generally more common than grysbok. The available faunal evidence suggests less contrast between the south-western and southern Cape during the late Pleistocene, probably in part because of greater climatic similarity and in part because faunal interchange was facilitated by exposure of the continental shelf during periods of lowered sea-level.

In the southern Cape, colder intervals during the Upper Pleistocene are clearly recorded in layers of frost-fractured debris at Nelson Bay Cave (Butzer 1973) and Die Kelders Cave 1 (Tankard 1976; Tankard & Schweitzer 1976), near both of which frost is unknown at present. Butzer's geomorphic research (Butzer & Helgren 1972; Butzer, Stuckenrath *et al.* 1978) suggests that the colder intervals were mainly drier, perhaps in large part because of the greater atmospheric stability promoted by weakening of the warm Agulhas Current off the southern Cape coast. A drier climate during colder intervals in the southern Cape is also indicated by Avery's (in prep.) analysis of the microfauna from Boomplaas Cave A.

Butzer has further detected a shift in geomorphic processes in the southern

Cape at about 4 200 B.P., reflecting relatively drier conditions in the early Holocene and more mesic ones subsequently. Pollen analysis of a Holocene sedimentary sequence at Groenvlei on the coastal fringe of the evergreen forest near Knysna may be read to support generally drier conditions in the early Holocene (Martin 1968).

The nature of Upper Pleistocene and Holocene environmental change in the south-western Cape is much less clearly established, and at least one of the Upper Pleistocene cold intervals may have been significantly moister, permitting the growth of yellowwood forest in areas today covered by sclerophyllous scrub (Schalke 1973; Coetzee 1978b).

The Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Cape Ecozone are listed in Table 7, along with the probable correlation of the sites (or of levels within them) with various oxygen-isotope stages. Although it is the smallest of the southern African ecozones discussed here, the Cape Zone contains the largest number of large, reasonably well-dated Upper Pleistocene and Holocene faunal samples, permitting a much more penetrating search for relationships between faunal change and environmental change established on other grounds.

In every Cape site that has provided large, thoroughly analysed late Pleistocene and Holocene faunal assemblages (Byneskranskop 1, Buffelskloof, Boomplaas, and Nelson Bay), the late Pleistocene assemblages contain a significantly higher proportion of large grazing ungulates, particularly alcelaphine antelopes and equids, suggesting that grasses were substantially more important in the regional vegetation during the late Pleistocene. The contrast is especially stark at Nelson Bay Cave, located on the coastal margin of the Knysna Forest, in an area where the principal ungulates recorded historically were bushpig, bushbuck, grysbok, and Cape buffalo. These are also the principal ungulate species in the Nelson Bay deposits postdating 11 000–10 000 B.P. Wildebeest, bontebok, springbok, quagga, and warthog were not present historically near the site and have not been found in deposits there that are younger than 11 000 years, yet they are the dominant species in deposits dating between 18 500 and 12 000 B.P. (the oldest fossiliferous ones at the site). This is probably the least equivocal faunal evidence for environmental change so far found at any Quaternary site in southern Africa. The presence of grassland interspersed with or largely in place of forest at Nelson Bay in the terminal Pleistocene is entirely compatible with Butzer's inference, based on geomorphic observations, that the terminal Pleistocene climate of the southern Cape was drier than the present one.

The faunas from earlier Upper Pleistocene cool or cold intervals also suggest a vegetation cover in which grasses were far more important than they were historically or than in intervening warmer intervals. The most important earlier Upper Pleistocene sites are the complex of caves at Klasies River Mouth, occupied by Middle Stone Age people shortly after a high sea-level which may be correlated with isotope stage 5e. This sea-level is clearly recorded in a beach

deposit on bedrock at Klasies Cave 1. On the basis of an analysis of the overlying Klasies sediments, especially the sand component, Butzer (1978a) has been able to establish the relationship between subsequent earlier Upper Pleistocene changes in sea-level (as reflected in the fluctuating distance between the sea and the site) and successive Middle Stone Age occupations. The sea-level changes were presumably of glacio-eustatic origin and therefore reflect global climatic events that are also reflected in the deep-sea oxygen-isotope stratigraphy. Oxygen-isotope determinations on (culturally accumulated) marine shells from various Klasies layers in fact indicate the expected correlation between higher off-shore water temperatures and higher sea-levels, as inferred by Butzer, and between cooler off-shore waters and lower sea-levels.

The Klasies sites are located on the eastern edge of the Knysna Forest, where the historic vegetation was a mosaic of evergreen forest, fynbos, and scrub in which the principal ungulates were Cape grysbok, blue duiker, bushbuck, bushpig, and Cape buffalo, much the same as at Nelson Bay, though unlike at Nelson Bay, the Cape hartebeest probably also occurred near by in fair numbers. In any case, the historically common ungulates clearly dominate the late Holocene deposits at Klasies and are also abundant in those earlier Upper Pleistocene layers formed when sea-level was high. In those earlier Upper Pleistocene levels formed when sea-level was low, wildebeest, bontebok, and an equid that is probably quagga are proportionately much more abundant, recalling the terminal Pleistocene fauna at Nelson Bay. Unfortunately, there is a large gap in the Klasies sequence from perhaps 65 000 to 5 000 B.P., so that the record of Upper Pleistocene faunal fluctuations near the site is not complete. Still, the fact that the faunal fluctuations which have been established correlate closely with environmental fluctuations established on other grounds and that they occur in a cultural context very different from that of Nelson Bay, clearly indicates that it was environment and not culture which was ultimately responsible for the faunal changes.

At Die Kelders Cave 1, the oldest stratigraphic unit is a boulder beach recording a sea-level not very different from the modern one. The beach is overlain by sterile quartzose sands overlain in turn by the first Middle Stone Age occupation. This earliest Middle Stone Age layer and a sterile layer immediately above it contain numerous angular, spalled flakes of roof rock that resulted from alternate freezing and thawing under much cooler climatic conditions than the modern ones (Tankard & Schweitzer 1976; Tankard 1976). Frost-fractured debris is also present in higher-lying Middle Stone Age layers, though less common, perhaps because fissures suitable for moisture penetration in the roof were largely removed by the initial freeze-thaw episode. Whatever the case, it is clear that much, if not all of the occupation of Die Kelders by Middle Stone Age people coincided with a distinctly cold interval, correlated here with oxygen-isotope stage 4 and perhaps part of 3, and the faunal sample is relatively rich in gregarious grazers, including some that were not recorded near the site historically and that have not been found in local Holocene faunas, including the one

TABLE 7

Upper Pleistocene and Holocene sites that have provided remains of large mammals in the Cape Ecozone.

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
<i>Isotope Stage 1, late (c. 5 000-0 B.P.)</i>			
De Hangen	Parkington & Poggenpoel (1971)	Q. B. Hendey, G. Avery, R. G. Klein	LSA
Paternoster	Robertshaw (1977)	R. G. Klein	LSA
Duiker Eiland	Robertshaw (in prep.)	R. G. Klein	LSA
Langebaan Lagoon	Robertshaw (1978)	R. G. Klein	LSA
Gordon's Bay Midden	Van Noten (1974)	A. Gautier	LSA
Die Kelders 1 (LSA levels)	Schweitzer (1970, 1974, 1975); Schweitzer & Scott (1973)	R. G. Klein & K. Scott	LSA
Byneskranskop Cave 1 (levels 1-5)	Schweitzer & Wilson (1978)	R. G. Klein (in press)	LSA
Buffelskloof (BOL)	Opperman (1978)	R. G. Klein (1978b)	LSA
Boomplass (DGL-FBL)	H. J. Deacon (1979); H. J. Deacon & Brooker (1976); H. J. Deacon <i>et al.</i> (1976, 1978)	R. G. Klein (1978c)	LSA
Nelson Bay Cave (Inskeep excavations)	Inskeep (1965, 1972)	R. G. Klein	LSA
Matjes River Mouth (layers A, B)	Louw (1960)	?	LSA
Andrieskraal 1	J. Deacon (1965)	Q. B. Hendey (Hendey & Singer 1965)	LSA
Andrieskraal 2	J. Deacon (1965)	Q. B. Hendey (Hendey & Singer 1965)	none
Scott's Cave	H. J. Deacon & J. Deacon (1963); H. J. Deacon (1967)	R. G. Klein & K. Scott (1974)	LSA
Klasies River Mouth (Cave 1/1-12; Cave 1D Cave 5/1-2)	Wymmer & Singer (1972); Butzer (1978a)	R. G. Klein (1976a)	LSA
<i>Isotope Stage 1, early (c. 12 000-5 000 B.P.)</i>			
Byneskranskop 1 (levels 19-6)	Schweitzer & Wilson (1978)	R. G. Klein (in press)	LSA

Buffelskloof (HE-MDA) Boomplaas (BRL7YA-BRL)	Opperman (1978) H. J. Deacon (1979); H. J. Deacon & Brooker (1976); H. J. Deacon <i>et al.</i> (1976, 1978)	R. G. Klein (1978b) R. G. Klein (1978c)	LSA LSA
Nelson Bay Cave (GSL-IC) Matjes River Mouth (layers C-E)	Klein (1972a, 1972b); J. Deacon (1978) Louw (1960)	R. G. Klein ?	LSA LSA
<i>Isotope Stage 1, undifferentiated (c. 12 000-0 B.P.)</i> Oakhurst Cave	Goodwin <i>et al.</i> (1938); Fagan (1960); Schrire (1962)	L. H. Wells (1960); R. G. Klein	LSA
Glentyre Shelter Kangara Cave	Fagan (1960) H. J. Deacon & Klein (unpub.)	L. H. Wells (1960) R. G. Klein	LSA LSA
<i>Isotope Stage 2 (c. 32 000-12 000 B.P.)</i> Boomplaas (BP-BRL7Y)	H. J. Deacon (1979); H. J. Deacon & Brooker (1976); H. J. Deacon <i>et al.</i> (1976, 1978)	R. G. Klein (1978c)	LSA and ?MSA
Nooitgedacht 1, 2 Nelson Bay Cave (YGL-BSL)	J. Deacon (1979) Klein (1972a, 1972b); J. Deacon (1978)	J. Brink & R. G. Klein R. G. Klein	none LSA
<i>Isotope Stages 3 and/or 4, undifferentiated (c. 75 000-32 000 B.P.)</i> Die Kelders Cave 1 (MSA layers)	F. R. Schweitzer (pers. comm.); T. P. Volman (in prep.); Tankard & Schweitzer (1974, 1976)	R. G. Klein (1975a)	MSA
<i>Isotope Stage 5a</i> Klasies River Mouth (Cave 1/13, Cave 1A/1-9)	Wymer & Singer (1972); Butzer (1978a)	R. G. Klein (1976a)	MSA
<i>Isotope Stage 5b</i> Klasies River Mouth (Cave 1A/10-21) Sea Harvest Faunal localities	Wymer & Singer (1972); Butzer (1978a) Hendey (1974); Northey (1979)	R. G. Klein (1976a) Q. B. Hendey; R. G. Klein; L. Northey	MSA none

SITE	GENERAL SOURCE	PERSON IDENTIFYING FAUNA AND SEPARATE PUBLICATION, IF ANY	ARCHAEOLOGICAL ASSOCIATIONS
<i>Isotope Stage 5c</i>			
Klasies River Mouth (Cave 1/14-37; Cave 1B/1-15; Cave 1C/36-37; Cave 5/5-7)	Wymer & Singer (1972); Butzer (1978a)	R. G. Klein (1976a)	MSA
Linkerhandgat-East and Windheuveld (Stamford)	H. B. S. Cooke (1955); Butzer (pers. comm.)	H. B. S. Cooke; R. G. Klein	none
<i>Isotope Stage 5d</i>			
Klasies River Mouth (Cave 1/38-39) Swartklip 1	Wymer & Singer (1972); Butzer (1978a) Hendey & Hendey (1968); Klein (1973c); Butzer (in prep.)	R. G. Klein (1976a) Q. B. Hendey & R. G. Klein	MSA none
<i>Isotope Stage 5e</i>			
Lake Pleasant (Groenvlei)	Butzer & Helgren (1972); Butzer (pers. comm.)	R. G. Klein	none
<i>Isotope Stage 5, unsubdivided</i>			
Herolds Bay	Brink & Binneman (unpub.); J. Deacon (1979)	Q. B. Hendey & J. Brink	none
<i>Isotope Stages 3, 4 and/or 5, undifferentiated</i> (c. 128 000-32 000 B.P.)			
Elandsfontein (in part)	Q. B. Hendey (1974); Inskeep & Hendey (1966)	Q. B. Hendey; L. H. Wells; A. W. Gentry; E. S. Vrba; R. G. Klein; R. Singer <i>et al.</i>	?MSA (in part) none (in part)
Bloembosch (possibly pre-5) Hoedjies Punt 1, 2 Ysterfontein	H. B. S. Cooke (1955) Northey (1979) G. Avery & Scott (unpub.); Northey (1979)	H. B. S. Cooke; R. G. Klein R. G. Klein; L. Northey R. G. Klein; L. Northey	? none none
Duinefontein 1 Duinefontein 4 Boomplaas (OLP-LOH)	R. G. Klein (unpub.) R. G. Klein (unpub.); Northey (1979) H. J. Deacon (1979); H. J. Deacon & Brooker (1976); H. J. Deacon <i>et al.</i> (1976, 1978)	R. G. Klein (incomplete study) R. G. Klein; L. Northey R. G. Klein (1978c)	none none MSA

from Die Kelders. As at Klasies, the Holocene fauna from Die Kelders dates from the later Holocene, and is unfortunately separated from the Middle Stone Age fauna by an occupation gap spanning several tens of thousands of years.

Finally, analysis of the aeolianite sequences at both Swartklip and Sea Harvest (Butzer pers. comm.) has indicated that the bone accumulations at both sites were formed during periods of lowered sea-level, in each instance probably reflecting major cool intervals within isotope stage 5. In historic times, the principal ungulates near each site were browsers and mixed feeders, but their fossil faunas are heavily dominated by grazers, many of which did not occur in the Cape Zone historically. The implication of a greater role for grasses is clear once again, and the fact that the faunal accumulations at both sites result from carnivore (v. human) activity further supports the notion that the long-term changes in the grazer/browser ratios described for Klasies, Nelson Bay, and other Cape Zone archaeological sites basically reflect changing environments and not changing cultural preferences and practices.

Besides Swartklip and Sea Harvest, there are several other probable carnivore sites in the south-western Cape in which the faunas are dominated by large grazers (Duinefontein 1 and 4, Elandsfontein 'bone circle', Ysterfontein, Hoedjies Punt 1 and 2), but these sites have not been firmly dated on independent grounds. They have therefore not been considered in greater detail here. The fact that grazer-dominated fossil faunas should be so common probably reflects the fact that climatic conditions cooler than present ones occupied much more of Upper Pleistocene time than conditions similar to present ones.

In the southern Cape, there is also one probable carnivore site (at Lake Pleasant) in which the fauna comes from deposits correlated with a warmer interval on independent geomorphic grounds, and although the faunal sample is small, it is probably significant that it contains no alcelaphine antelopes or equids, but that Cape buffalo is represented and dolphin is present, indicating proximity of the sea. The fauna from Bloembos near Darling in the south-western Cape may also date from a warmer interval(s), though possibly a mid rather than Upper Pleistocene one. The Bloembos fauna is especially interesting because it contains the only Pleistocene record of a giraffe in the Cape Zone, and Bloembos is presently located in an area where trees were unknown historically. By itself, giraffe implies a very different environment from the recent one.

One apparent anomaly in all the Upper Pleistocene faunas of the Cape Zone that are especially rich in grazing ungulates is the rarity or absence of steenbok, though grysbok is always present (Klein 1975*b*). Steenbok is much better represented in the browser-dominated Holocene and historic faunas of the region, especially in the south-western Cape, where it often outnumbers grysbok locally. This seems the opposite of what would be expected, since, between the two, it is the steenbok which eats more grass and which might therefore have profited more from grassier vegetation. However, the steenbok is also highly dependent on browse, and the answer to the puzzle is probably the nature of the

available browse during cooler, grassier intervals. The grysbok is basically a Cape Zone endemic, and its evolutionary origins and history may well be linked to its ability to make maximum use of those browse plants which remained during the substantial periods when grasses became more common as a result of climatic change. Details of the browse preferences of grysbok v. steenbok in areas where they overlap today might well provide clues as to what browse plants disappeared or became much rarer during Pleistocene cold intervals. More generally, when they can be distinguished osteologically, fluctuations in the relative frequencies of closely related pairs of species such as steenbok and grysbok probably have considerable potential for providing fine detail on past environmental changes.

Klasies, Nelson Bay, Die Kelders, Swartklip, and Sea Harvest are all coastal sites whose faunal contents could be expected to reflect Upper Pleistocene and Holocene changes in sea-level. The late Pleistocene/early Holocene rise in sea-level is, in fact, very clearly reflected in the Nelson Bay sequence in which shells or bones of marine animals do not occur in the deposits dating to between 18 500 and 12 000 B.P. Marine creatures, including the Cape fur seal, appear only in deposits dated to about 12 000, when the coastline had moved to within 10 km of the site, and they become especially abundant in deposits younger than 10 000 B.P., after which the sea was always within easy striking distance. The same phenomenon is recorded in the terminal Pleistocene/early Holocene sequence at Byneskranskop 1, though seal bones are less common throughout, presumably because the site has never been directly on the coast (it is presently about 6 km away).

The marine regressions that occurred during the earlier Upper Pleistocene (Middle Stone Age) occupations at Klasies River Mouth are known to have been less dramatic than the terminal Pleistocene one, and this is apparently reflected in the presence of seal bones and other marine food debris throughout the Klasies sequence. There is, however, a tendency for seals to be less well represented in layers formed during regressive phases. Less dramatic regression, in combination with a steeply sloping continental shelf immediately off shore at Die Kelders, is perhaps also responsible for the occurrence of seal bones throughout the Middle Stone Age occupation there. It is probably significant that seal bones are less common in the Middle Stone Age levels than in the late Holocene ones, formed when the sea lapped virtually at the mouth of the cave, as it does today.

At Swartklip, marine creatures are completely absent, perhaps implying a more substantial regression than at Sea Harvest where seals and other marine creatures are represented in small quantities. Again, the continental shelf immediately off Sea Harvest is relatively steep, so that substantial regression would be necessary to remove the sea completely from the rounds of its (?)hyaena inhabitants. It is interesting that where seal bones do occur in Cape Zone deposits apparently dating from a relatively cool interval, antarctic and sub-antarctic seals (especially elephant seal, but also gazelle seal and crab-eater)

appear to be relatively better represented than in deposits from warmer intervals in which Cape fur seal is often the only pinniped present.

The relatively large faunal samples available from the Holocene levels at Nelson Bay are less different from one another than are any of them from the late Pleistocene samples, but they are still characterized by significant change through time. Thus, in addition to grysbok, bushbuck, Cape buffalo, and bushpig, the early Holocene samples dating between roughly 10 000 and 5 000 B.P., are relatively rich in remains of vaalribbok, mountain reedbuck, and roan antelope. In deposits postdating 5 000 B.P., remains of these creatures are much rarer, and the blue duiker, well known in the area historically, makes its first appearance. The precise timing of the faunal shift will probably become clearer as a result of excavations recently completed by R. R. Inskeep in Nelson Bay deposits dating between 5 000 and 3 000 B.P. The implications of the shift are not entirely clear, but broad coincidence with the change in geomorphic processes identified by Butzer at c. 4 200 B.P. suggests that it reflects an environmental change, perhaps the establishment of the Knysna Forest in essentially its historic form.

Environmental differences between the earlier and later Holocene are also suggested by differences between the faunal samples from the corresponding levels of Boomplaas Cave A. The faunal differences are at least broadly correlated with differences in the proportions of tree species represented by charcoals (H. J. Deacon 1979). In recent times, the most important source of firewood in the vicinity has been the thorn tree, *Acacia karroo*. It is also the principal tree represented by charcoals in the late Holocene deposits of the site, but it is far less common in the earlier Holocene levels, and it is not represented at all in the late Pleistocene levels, where the principal trees providing charcoal were olive spp. Both olive and thorn trees have dense wood that produces good charcoal, and the change through time almost certainly reflects long-term change in the vegetation rather than changing cultural preferences. Studies of pollens currently under way should shed more light on the nature of the vegetational change and its relationship to contemporaneous faunal changes at Boomplaas.

CONCLUSIONS

Changes in large mammal distributions or species frequencies that probably reflect Upper Pleistocene and Holocene environmental change can be demonstrated to some extent in all the ecozones of southern Africa. However, a pattern of change in mammalian faunas that can be compared to patterns of long-term environmental change established on other grounds can be demonstrated only in the Cape Zone, where cooler intervals repeatedly witnessed an increase in grazing ungulates relative to browsers. In part, the failure to demonstrate comparable patterns in other zones may reflect the fact that Upper Pleistocene environmental and faunal change was greater in the Cape Zone than elsewhere, but in part it almost certainly also reflects the better overall quality of data from the Cape—more well-dated sites and more relatively large faunal assemblages

for which detailed numerical data are available. Some authorities believe that it is not really possible to use fossil faunas to document environmental change because it is rarely possible to know the relationship between relative species abundance in a fossil fauna and relative abundance in the live fauna from which the fossils were derived. However, the Cape data show that this is not an insuperable problem, and the contrast between the Cape Zone and others indicates that widespread deficiencies in dating, sample size, and sample description are far more serious obstacles to the palaeoenvironmental interpretation of faunal data.

MAMMALIAN EVIDENCE FOR CULTURAL CHANGE

In archaeological sites, changes in environment and changes in culture are the principal causes of shifts in relative species abundance through time. In situations where the intervals between shifts represent thousands of years, where the shifts are repetitive or cyclical, where they appear to be correlated with changes in environment suggested by other lines of evidence, and where they occur in the absence of evidence for any significant cultural change or innovation, the writer feels it is most economical to ascribe the species fluctuations to environmental change. Most of the fluctuations in large mammal frequencies that can be documented through Upper Pleistocene and Holocene time in southern Africa seem to the writer to occur in circumstances such as the ones that have just been listed, and they have therefore been discussed in the previous section on 'Mammalian Evidence for Environmental Change'. There are, however, some instances of mammalian frequency changes which are not clearly related to environmental change, which are not repetitive or cyclical, and which occur in contexts where there is evidence for major cultural change or innovation.

The most obvious instance of a culturally determined species frequency change is the introduction of domestic stock to southern Africa by Iron Age mixed farmers, beginning about 2 000 years ago (Phillipson 1977). The stock were diffused far beyond the areas ever occupied by Iron Age farmers themselves (H. J. Deacon *et al.* 1978, with references), and some of the late Holocene faunas listed in the last section may be used to establish the route(s) of diffusion (Klein 1979a) or the impact the stock may have had on the abundance of some indigenous wild species (Klein 1974b). For the open grasslands of the Basutolian region, Maggs (1975) has documented faunal differences that probably reflect major social and technological differences between Iron Age people and broadly contemporaneous Stone Age ones in the same area. The Iron Age faunal samples are richer in large gregarious grazing ungulates, probably because Iron Age peoples could mobilize more manpower for surrounds and drives and could more easily dig game pits that, combined with drives, would constitute the most effective means of obtaining large ungulates in the Basutolian Zone.

The principal concern in this section, however, is not with changes in species frequencies that reflect the introduction of domestic stock or of Iron Age technology and social organization, but rather with a much earlier, more subtle

shift in mammal species frequencies that the writer believes may reflect important differences between Middle Stone Age and Later Stone Age peoples in their ability to hunt.

In southern Africa, the term Middle Stone Age (MSA) is currently applied to artefact assemblages dominated by large stone flakes and blades, sometimes altered by retouch into side-scrapers, end-scrapers, points, denticulates, notches, backed pieces, and other tool types conventionally recognized by archaeologists. Handaxes are absent, and microlithic tools are rare. Bone artefacts are also rare, and items of personal adornment or art objects are unknown. Typological and technical variability through space and time is relatively limited, and many differences in typology or flaking technique among MSA assemblages in different regions or at different times may reflect differences in raw material availability more than anything else. The earliest Middle Stone Age assemblages in southern Africa may be as much as 200 000 years old (Butzer, Beaumont & Vogel 1978), while the latest are probably all older than 30 000 years, on the basis of a large series of recently obtained radiocarbon dates (see especially Vogel & Beaumont 1972; Beaumont *et al.* 1978; H. J. Deacon 1979; Klein 1974a).

It is presently impossible to characterize the Later Stone Age (LSA) succinctly, in part because the artefact assemblages involved are more variable in time and space than Middle Stone Age ones and in part because only Later Stone Age assemblages post-dating 20 000 B.P. are reasonably well known. LSA assemblages ante-dating 20 000 years have been found at only a handful of sites in southern Africa (Kalemba, Leopard's Hill, Redcliff, Heuningsneskrans, Border Cave, Apollo 11, Elands Bay, and Boomplaas; with references in Tables 2-7), where the samples are either small or remain incompletely described or both. In most LSA assemblages post-dating 20 000 B.P., microlithic tools are a prominent component, but this is not universally true, and, in the Cape Ecozone, there is clear evidence for a 'macrolithic' industry sandwiched between two 'microlithic' ones (J. Deacon 1978). Generally speaking, LSA peoples appear to have produced 'macrolithic' flakes and blades with less care than many MSA peoples. At least the better known LSA assemblages younger than 20 000 B.P. also regularly include standardized bone artefact types (such as 'awls', 'points', 'needles', 'hide-burnishers', and 'fish-gorges'), as well as easily recognizable items of personal adornment or art objects (ostrich egg-shell beads, incised or engraved pieces of ostrich egg-shell or bone, shell pendants, etc.). On the evidence from Border Cave, it seems likely that the manufacture of beads and standardized bone artefacts was practised from the very beginning of the Later Stone Age, more than 30 000 years ago. People making Later Stone Age artefacts of various kinds were still living in much of southern Africa at time of historic contact.

The available evidence suggests strong parallels between the Middle Stone Age and Later Stone Age of southern Africa, as outlined here, and the Middle Palaeolithic (Mousterian) and Upper Palaeolithic of Europe, as they have long

been known. Although the Middle Stone Age may have begun somewhat earlier than the Middle Palaeolithic, throughout much of their existence the two were clearly contemporaneous and their terminal dates are very similar. Both exhibit less temporal and spatial variability than the culture-stratigraphic units that succeed them, and both are characterized by the absence of art objects and standardized bone artefact types. One major point of non-comparability may be in the kinds of people associated with them. While the makers of Middle Palaeolithic artefacts were Neanderthals (*Homo sapiens neanderthalensis*), clearly distinct from modern people, the makers of MSA tools may have been anatomically modern (*Homo sapiens sapiens*) (Rightmire 1979), though a pattern of well-documented associations between MSA artefacts and diagnostic human remains will be necessary to show this with reasonable certainty. The makers of Upper Palaeolithic artefacts were certainly anatomically modern, as were at least those Later Stone Age people who lived after 20 000–18 000 B.P.

In Europe, there is substantial evidence to argue that the Upper Palaeolithic represents a quantum advance over what preceded it (Klein 1973), and at least for the moment, the writer feels it is reasonable to hypothesize that the Later Stone Age represents basically the same phenomenon in southern Africa. Under these circumstances, differences between MSA and LSA faunas from sites occupied under broadly similar environmental conditions could be interpreted to reflect cultural evolution. In order to establish such faunal differences, it is of course necessary to have large MSA and LSA faunal samples whose palaeo-environmental context has been reasonably well established on independent grounds, and these conditions are so far met only in the Cape Ecozone, especially by the Middle Stone Age faunas from Klasies River Mouth and Die Kelders 1 and the Later Stone Age ones from Nelson Bay Cave and Byneskranskop 1.

At all four sites, in levels that were formed when the coast was at or near its present position, bones of seals and penguins are common, but only in the two Later Stone Age sites are they accompanied by large numbers of bones from fish and from flying marine birds. The writer believes this indicates that Later Stone Age people were capable of active fishing and fowling, while Middle Stone Age people were not. With regard to the terrestrial mammal remains that are the principal focus of this paper, there is also an interesting contrast. Comparing layers at Nelson Bay formed during the Holocene to ones that appear to have formed during broadly similar portions of the Last Interglacial at Klasies, the Nelson Bay deposits are significantly richer in remains of pigs and poorer in remains of eland. The LSA levels of Byeneskranskop 1 contrast with the MSA ones at Die Kelders in essentially the same way (the comparisons here are restricted to pairs of sites which are located in very similar environments today), though the extent of past environmental comparability is less certain than in the Klasies/Nelson Bay case. In any event, the writer has suggested that the higher frequency of wild pig and lower frequency of eland in the LSA sites reflects the enhanced ability of LSA people to deal with prey that are likely to mount an effective counter-attack on the hunter. Using data on the ages of animals

represented in the Nelson Bay and Klasies faunas in addition to the contrasts in relative species frequencies, the writer has further suggested that even when MSA people hunted basically the same species as their LSA successors, they were less effective, that is, they took a smaller proportion of the available animals (Klein 1979b).

Clearly, the hypothesis that LSA hunters were more effective than MSA ones would be more secure if it could be demonstrated at additional sites in the Cape Zone and also at sites outside it. The writer has examined the available faunal data from all the other ecozones considered in the previous section of this paper, and only in the Zambesian Zone are there sufficient numerical data for even a preliminary test. Pigs (especially warthog) are more common in both MSA and LSA sites in the Zambesian Zone than in contemporaneous Cape sites, probably reflecting the fact that pigs have always been more abundant in the Zambesian Zone, as they were historically. At the same time, in those Zambesian sites for which numerical data are available, pigs are relatively more frequent in LSA levels (Kalemba, Redcliff, Gwisho, Leopard's Hill, and Makwe) than in MSA ones (Kalemba and Redcliff). However, at Redcliff and Kalemba, where MSA and LSA pig frequencies may be compared within the same sites, the relative increase in pigs is not statistically significant, and it remains possible that the observed differences in pig frequencies between the MSA sites and various LSA ones reflect differences in local environment rather than cultural evolution. Sorting out the alternatives will be possible only with better palaeo-environmental controls and larger faunal samples. More generally, as in the case of environmental change, the principal obstacle to documenting cultural change from large mammal remains is the shortage of appropriately large, well-described, and well-dated samples.

THE ECOLOGY AND DEMISE OF EXTINCT SPECIES

Not very long ago, it was widely believed that Acheulean cultures had survived into the Upper Pleistocene and that faunas associated with later Acheulean artefacts could even be as recent as 40 000 B.P. The richest such fauna in southern Africa is the one from Elandsfontein (Hopefield) in the south-western Cape Province (Hendey 1974 with references), which is characterized by at least 19 extinct large mammal species out of approximately 50 that have been identified. The extinct species include a giant gelada baboon (*Theropithecus* (*Simopithecus*) sp.), a sabre-toothed cat (*Megantereon* sp.), an elephant (*Loxodonta atlantica*), a large horse or zebra (*Equus capensis*), two different kinds of pigs (*Mesoscoerus* sp. and *Metridiochoerus* sp.), a sivathere (*Sivatherium maurusium*), a small kudu (*Tragelaphus* (*Strepsiceros*) sp.), a giant buffalo (*Pelorovis* sp.), a giant hippotragine antelope (*Hippotragus gigas*), the ancestor (*Rabataceras arambourgi*) of the modern hartebeests, an extinct bastard hartebeest (*Damaliscus niro*), a giant alcelaphine antelope (*Megalotragus* sp.), a large grysbok (*Raphicerus* sp.), a gazelle (*Gazella* sp.), springboks (*Antidorcas recki*

and *A. australis*), and some peculiar antelopes whose affinities will perhaps be clarified following E. S. Vrba's current detailed study of the Elandsfontein bovids.

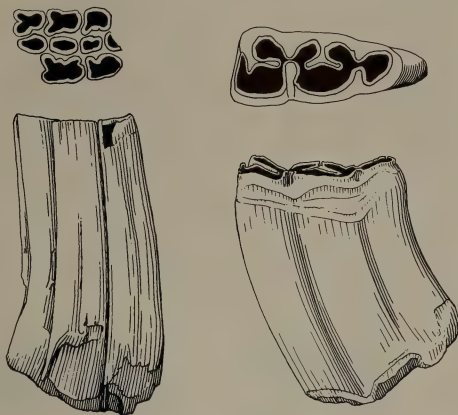
It is now very clear that the Acheulean did not survive into the Upper Pleistocene, and it seems increasingly probable that it was replaced by the Middle Stone Age within the later part of the Middle Pleistocene, more than 130 000 years ago (Klein 1976b; Butzer, Beaumont & Vogel 1978; Szabo & Butzer 1979). Furthermore, the overwhelming majority of extinct species represented at Elandsfontein and other Acheulean sites are not represented in Middle Stone Age faunas and in non-archaeological faunas that are contemporaneous with them (see the lists of sites in Tables 2-7 above). Particularly striking in this context is the absence of most of the extinct Elandsfontein species in large earlier Upper Pleistocene faunas in the (same) Cape Ecozone, especially in the very large samples from Klasies River Mouth, where dating of the MSA artefacts and associated fauna to the early Upper Pleistocene is secure. In fact, it appears increasingly likely that most of the extinct species present at Elandsfontein and other Acheulean sites disappeared well before the early Upper Pleistocene, since they are not represented in the large faunal sample from Florisbad, most of which probably comes from a later mid-Pleistocene horizon at the site (Butzer pers. comm.).

The Florisbad fauna contains five extinct species of large mammals—the 'giant Cape horse' (*Equus capensis*), a large warthog (*Metridiochoerus* sp.), a giant buffalo (*Pelorovis antiquus*), a giant alcelaphine (*Megalotragus priscus*), and Bond's springbok (*Antidorcas bondi*). With the addition of the southern springbok (*Antidorcas australis*), these are also the only extinct species which have been found in Upper Pleistocene contexts in southern Africa. Some identifications assigned to the extant *Damaliscus dorcas* (bontebok/blesbok) in Upper Pleistocene faunas may actually belong to the extinct form *Damaliscus niro*, but horn-cores to prove the presence of *D. niro* are lacking. Additionally, in contrast to Gentry (1978), the writer believes that *D. niro* may be ancestral to Upper Pleistocene and recent *D. dorcas*, in which case it is not extinct in the same sense as the other species considered here. Extinct forms of wildebeest and reedbuck are common in Upper Pleistocene sites in the Cape Ecozone, but were probably just local variants (subspecies) of the black wildebeest and southern reedbuck that survived elsewhere.

The purpose in this section is to present the information that is available on the distribution and ecology of the extinct species followed by a brief consideration of the causes of extinction. Teeth of the various extinct forms are illustrated in Figures 3-5.

EQUUS CAPENSIS

The writer has followed Churcher & Richardson (1978; also Churcher 1970) in assigning all large later Pleistocene horses in southern African sites to the species *Equus capensis* (including '*E. helmei*', '*E. plicatus*', et al.) Upper Pleistocene specimens assignable to *Equus capensis* have been found in all six ecozones



***Metridiochoerus* sp.**
(RC VII EE I)

Equus capensis
(RC VI S)

Fig. 3. A fragmentary third molar of *Metridiochoerus* sp. and a lower third molar of *Equus capensis*. Both specimens come from Redcliff Cave, Zimbabwe Rhodesia, and are reproduced natural size. (Drawings by K. Scott.)

considered earlier: at Redcliff in the Zambesian Zone; at Pomongwe, Chelmer, Kalkbank, the Cave of Hearths, Bushman Rock Shelter, Border Cave, and Aloes in the Transvaalian Zone; at Equus Cave, Black Earth Cave, and Ng in the Kalaharian Zone; at Florisbad, Vlakkraal, and Koffiefontein in the Basutolian Zone; at Apollo 11 and Elands Bay Caves in the Karoo-Namaqualian Zone; and at Sea Harvest, Hoedjies Punt, Swartklip, Bloembos, Duinefontein, Byneskranskop 1, and Boomplaas in the Cape Zone.

On the evidence from Apollo 11, Elands Bay, Byneskranskop 1, and Boomplaas, *Equus capensis* probably made its last appearance in the Karoo-Namaqualian and Cape Zones between 12 000 and 10 000 years ago. In the Zambesian Zone, it is known from the 'Tshangula' horizons at Redcliff, where it may be as young as 20 000 B.P. In other zones, it cannot be shown to have survived 40 000–30 000 B.P., but this probably reflects the very small number and small size of faunal samples that date between 40 000–30 000 and 10 000 B.P.

in these zones. In essence, the time when *E. capensis* made its last appearance outside the Karoo-Namaqualian and Cape Zones remains to be established.

In most Upper Pleistocene sites in southern Africa and in all those which have provided large samples, *Equus capensis* is accompanied by one or more of its smaller, historic relatives—Burchell's zebra, quagga, or mountain zebra. In most sites, it is much less common than the smaller form(s), but in Karoo-Namaqualian sites, located in what is and perhaps always has been the driest of the southern African ecozones, and in sites in the drier, western portion of the Cape Ecozone, it is relatively more common (versus smaller equids). Additionally, in the Zambesian Zone, at Redcliff, where *E. capensis* is not particularly frequent overall, it is most frequent in the 'later Bambata' horizons, which sedimentological evidence suggests were formed under comparatively arid conditions. The possibility that *E. capensis* preferred or was relatively well adapted to arid environments is especially interesting, since some authorities believe it was ancestral to the living Grevy's zebra of northern Kenya, southern Ethiopia, and Somalia (Churcher & Richardson 1978). Among the living zebras,

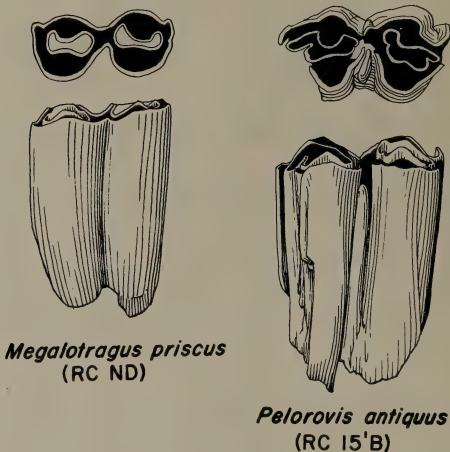


Fig. 4. Lower molars of *Megalotragus priscus* and *Pelorovis antiquus*. Both specimens come from Redcliff Cave, Zimbabwe Rhodesia, and are reproduced natural size. (Drawings by K. Scott.)

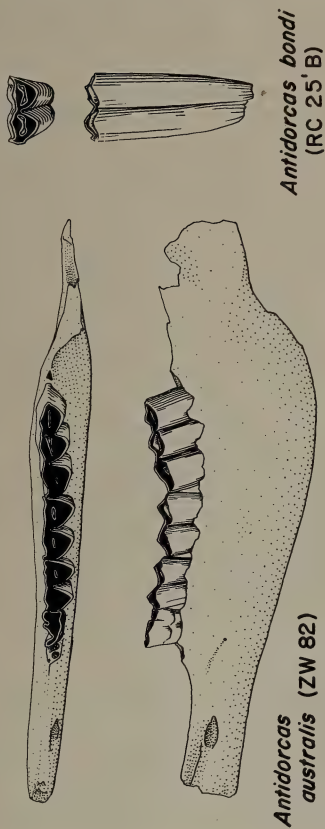


Fig. 5. A mandible of *Antidorcas australis* from Swartklip 1, south-western Cape Province, South Africa, and a lower molar of *Antidorcas bondi* from Redcliff Cave, Zimbabwe Rhodesia. Both specimens are reproduced natural size. (Drawings by K. Scott.)

Grevy's appears to be the least dependent upon water. It inhabits some of the most arid country in east Africa, overlapping Burchell's zebra on the margins of its range, but occurring alone in the arid core.

METRIDIOCHOERUS SP.

The writer has followed White and Harris (1977) in assigning all large warthog-like pigs of the later Pleistocene to the genus *Metridiochoerus* (including '*Stylochoerus*', '*Tapinochoerus*', *et al.*), though not all specialists agree with their taxonomy (Cooke 1978). In any case, the large pigs involved are so far very rare in Upper Pleistocene contexts, having been recorded only at Koffiefontein, Vlakkraal, and Florisbad in the Basutolian Ecozone (the Florisbad specimens may be largely or wholly of mid-Pleistocene age), and at Redcliff Cave in the Zambesian Zone. Among these occurrences, the latest is perhaps at Redcliff, where a large warthog-like pig is still present in the 'Tshangula' horizons, tentatively dated to between 30 000 and 20 000 B.P. in discussion above.

Estimates of *Metridiochoerus* abundance are available only from Redcliff where the creature is very rare, too rare to search for frequency covariation with extant species that might indicate shared habitat preferences. Its highly hypsodont molars, similar in structure to those of the warthog, plainly indicate it was a grazer, which is in keeping with the predominance of grazers at Redcliff and in the Basutolian faunas in which *Metridiochoerus* has been identified.

PELOROVIS ANTIQUUS

The writer has followed Gentry (1978) in assigning all the 'giant', long-horned Upper Pleistocene buffaloes of southern Africa to this species (including especially material formerly assigned to '*Homoioceras baini*'). Fossils of *Pelorovis antiquus* have been found at Redcliff in the Zambesian Zone; at Kalkbank and the Cave of Hearths in the Transvaalian Zone; at \neq gi in the Kalaharian Zone; at Florisbad, Vlakkraal, Koffiefontein, and Driefontein in the Basutolian Zone; at Elands Bay Cave in the Karoo-Namaqualian Zone; and at Sea Harvest, Hoedjies Punt, Ysterfontein, Bloembos, Swartklip, Die Kelders, Nelson Bay, Boomplaas, and Klasies River Mouth in the Cape Zone. The species was thus very widespread, but it is generally not common in fossil faunas, except in the Basutolian Zone, where it has also been recorded as an apparently isolated fossil at various localities, for example, in the alluvium of the Modder River, which provided the first giant buffalo fossil to be scientifically recorded in southern Africa (Cooke 1955).

Finds at Nelson Bay and Elands Bay Caves suggest *P. antiquus* made its last appearance in the Cape and adjacent parts of the Karoo-Namaqualian Zone between 12 000 and 10 000 years ago. Elsewhere, it cannot be shown to have survived beyond 40 000–30 000 B.P., but, as in the case of *Equus capensis*, this probably reflects the absence of large faunal samples from the interval between 40 000–30 000 and 10 000 B.P. The date of its last appearance outside the Cape and Karoo-Namaqualian Zones thus remains to be established.

The hypsodont teeth and exceptionally long horns of *P. antiquus* (spanning

2-3 m) both point to a preference for relatively open, grassy environments, also perhaps suggested by the relative abundance of the species in Basutolian sites. It seems likely that *P. antiquus* was more at home in open settings than its closest living relative, the Cape buffalo. Ecological distinction from the Cape buffalo is implied at Klasies River Mouth, where the frequencies of the two species vary independently of one another from level to level within the deposits. At Klasies, the frequency of giant buffalo is correlated most closely with that of eland, which may suggest a common environmental preference. Eland, as studied by Hillman (1974), appear to favour open country with large islands and galleries of tree and shrub growth. The Basutolian sites at which giant buffalo are common are all located near streams or springs where such islands or galleries probably occurred. The giant buffalo may have gravitated to them for shade rather than for food.

At Klasies, there are enough giant buffalo dentitions for an analysis of the ages at which individual animals died or were killed by the Middle Stone Age occupants of the site (Klein 1978*d*, 1979*b*). Most of the individuals present were within the first 10 per cent of potential lifespan (many were newborn), while among older animals, prime adults (between 20% and 50% of lifespan) were especially rare. The Klasies giant buffalo age distribution is very similar to the natural (attritional) mortality pattern in all free-ranging large ungulates, to the age distribution in recently observed Cape buffalo killed by lions, and to the age distribution of Cape buffalo in the same Klasies MSA levels. Recent observations indicate that it is large size and membership in large herds that make Cape buffalo prime adults largely immune to lion predation. The age distribution of Cape buffalo at Klasies suggests that the MSA occupants were constrained by the same features as lions in dealing with Cape buffalo, and the similarity between the Cape buffalo and giant buffalo distributions suggests that large size and herd membership may also be the reasons that giant buffalo prime adults are rare at Klasies. Given the resemblances between the giant buffalo age profile at Klasies and the probable natural (attritional) mortality pattern in giant buffalo, it is even conceivable that the Klasies people did not prey on giant buffalo at all, but scavenged individuals which had died naturally or been killed by other predators.

MEGALOTRAGUS PRISCUS

The writer has followed Gentry (1978) in assigning all the later Pleistocene 'giant alcelaphines' of southern Africa to the single species *Megalotragus priscus* (including '*Peleroceus*' spp, '*Lunatoceras mirum*', '*Alcelaphus helmei*', et al.). Upper Pleistocene fossils of *M. priscus* have been found at Leopard's Hill and Redcliff in the Zambesian Zone; at Chelmer and Kalkbank in the Transvaalian Zone; at Equus Cave, Black Earth Cave, Gobabis, and \neq gi in the Kalaharian Zone; at Florisbad, Vlakkraal, Koffiefontein, and Driefontein in the Basutolian Zone; and at Hoedjies Punt, Boomplaas, and Nelson Bay Cave in the Cape Zone. Outside the Basutolian Zone, *M. priscus* is generally not a common

element in fossil faunas; within this zone, it is not only well represented at the sites listed above but has been found as an isolated fossil or with presently unclear associations at a variety of other sites, including especially the alluvium of the Modder River, which provided the holotype specimen.

Its hypsodont teeth, the dietary preferences of all its closest living relatives (hartebeests, wildebeests, and bastard hartebeests), its former distribution, and its clear tendency to be most common in fossil faunas heavily dominated by grazers, indicate beyond all doubt that *M. priscus* was a grazer. Its latest known occurrence is in deposits at Nelson Bay Cave radiocarbon-dated to approximately 16 000 B.P., but it is a rare element in the Nelson Bay fauna, and the possibility is good that it persisted, like *Equus capensis* and *Pelorovis antiquus*, in the Cape Zone somewhat later, perhaps to between 12 000 and 10 000 B.P. At Leopard's Hill in the Zambesian Zone, its provenience within the site is uncertain, but it is almost certainly younger than 24 000 radiocarbon years (the approximate age of the oldest fossiliferous deposits at the site). Elsewhere, it cannot be shown to have survived beyond 40 000–30 000 B.P., but again, as in the case of *Equus capensis* and *Pelorovis antiquus*, this may well reflect the rarity of large faunal samples from the interval 40 000–30 000 to 10 000 B.P., rather than the absence of the species.

ANTIDORCAS BONDI

Cooke and Wells (1951) initially described this hyperhypsodont antilopine antelope as *Gazella bondi*. However, Vrba (1973) has demonstrated that the frontals of this species were inflated below the horn-cores, a feature that is characteristic of *Antidorcas* and not of *Gazella*. For this and other reasons, the species is better placed in *Antidorcas* (Gentry 1978).

Upper Pleistocene fossils of *A. bondi* are known from Redcliff in the Zambesian Zone; from Chelmer, the Cave of Hearths, and Border Cave in the Transvaalian Zone; from Gobabis, Witkrans, Equus Cave, and Black Earth Cave in the Kalaharian Zone; and from Florisbad, Vlakkraal, and Driefontein in the Basutolian Zone. Its absence so far in the Karoo–Namaqualian Zone may be a result of inadequate sampling, but its failure to occur in Cape faunas may reflect true absence, since the Cape samples in which it might be expected are relatively large.

The latest record of *A. bondi* is at Border Cave in a level radiocarbon-dated to approximately 38 000 B.P. However, the date of its last appearance remains unestablished, since large samples dating to between 38 000 and 10 000 B.P. are unknown in those ecozones where the species was most common.

Its hyperhypsodonty, geographic distribution, and the species with which it occurs all indicate clearly that *A. bondi* was primarily a grazer. This is shown particularly well at Border Cave, where there is alternation between levels dominated by grassland species and ones dominated by species that prefer bushier settings. *A. bondi* is plainly most common in those levels where grassland animals are most abundant.

ANTIDORCAS AUSTRALIS

Hendey and Hendey (1968) originally described this species as a subspecies of the common springbok, *Antidorcas marsupialis*. However, Hendey (1974) concluded it was more likely to be a separate species, since, at the mid-Pleistocene locality of Elandsfontein, it was apparently sympatric with *A. recki*, the probable ancestor of the common springbok. Upper Pleistocene fossils of *A. australis* have been found only in the Cape Ecozone where it was widespread. Its last recorded occurrence is in deposits at Nelson Bay Cave dated to between 12 000 and 10 000 B.P.

A. australis had horn-cores that were more mediolaterally compressed than those of *A. marsupialis* and that did not bend sharply backwards and outwards. It was also somewhat smaller on average than *A. marsupialis*, but in most other important respects, including the morphology of the dentition, it was very similar to *A. marsupialis*. *A. marsupialis* is not known to have occurred in the Cape Zone in Upper Pleistocene (or recent) times, except on the peripheries, and it seems likely that *A. australis* filled the niche for a small selective grazer also capable of some browsing that *A. marsupialis* filled and still fills in neighbouring ecozones. Like the frequency of *A. marsupialis*, that of *A. australis* in fossil sites is closely linked to the frequency of 'plains' species, such as wildebeest, bastard hartebeest, and zebra.

THE CAUSES OF EXTINCTION

As in other parts of the world, the causes of late Pleistocene mammalian extinctions in southern Africa are a subject of considerable interest, particularly given the very real possibility that early people were involved. The other major 'cause' which has been postulated is environmental change.

The writer believes that environmental change played a role in late Pleistocene extinctions, but it can nowhere be the sole reason, since the species that became extinct repeatedly survived the same kinds of environmental change earlier on in the Pleistocene. This can be shown especially clearly in the Cape Ecozone where the extinction of the giant Cape horse, giant buffalo, southern springbok, local subspecies of the black wildebeest and southern reedbeek, and probably also the giant alcelaphine occurred roughly 12 000–10 000 years ago, at a time when it is clear that fynbos, bush, and forest were replacing much of the grassland that had existed previously. The species that disappeared were all primarily grazers, which probably did suffer a shrinkage in both numbers and range as a result of the vegetational change. However, the same kind of vegetational change characterized similar climatic shifts earlier on in the Cape Zone (that is, earlier transitions from 'glacial' to 'interglacial' conditions). During these earlier shifts, at least some of the extinct species appear to have become less numerous, but they all survived.

Environmental change is thus not a sufficient explanation for extinctions in the Cape Zone, and the principal factor which differentiated the period of extinction, 12 000–10 000 years ago, from earlier periods of comparable

environmental change was perhaps the presence of more proficient hunters, as discussed in the previous section of this paper. The writer believes that it is entirely possible that Stone Age people in the Cape, faced with a decline in the 'plains' game on which they had depended for generations, intensified their pursuit of those that were left, perhaps through technological innovation driving the numbers of some species below a critical threshold and impairing their reproductive capacity. Extinction would follow, even if people were not responsible for killing the very last animal.

Outside the Cape Ecozone, the hypothesis that people were responsible for late Pleistocene extinctions is much more tenuous. It seems likely that the extinctions occurred after Later Stone Age peoples had replaced Middle Stone Age ones in other ecozones, but evidence that these Later Stone Age peoples were more proficient hunters is so far lacking. Additionally, the timing of extinctions outside the Cape Zone remains unclear, mainly because there are no large faunal assemblages elsewhere dating from the critical period between 40 000–30 000 and 10 000 B.P. Finally, even if it is assumed that the extinctions outside the Cape Zone took place 12 000–10 000 B.P., as they did inside it, the nature of environmental change in this interval is not as well established as in the Cape, and it is far from certain that it would have adversely affected the extinct species in the way it probably did in the Cape. This is important, because the hypothesis offered above requires an environmental stimulus for any human role in extinction.

Clearly, further elucidation of the causes of late Pleistocene extinctions in southern Africa will require the recovery of large late Pleistocene faunal samples from various ecozones. These are necessary not only for more precise estimates of the timing of extinctions and of the nature of any environmental change that may have accompanied them, but also for determining if the extinct species experienced long periods of decline or if they disappeared rather abruptly, as appears to be the case in the Cape Zone. Additionally, large samples may allow the construction of age/sex profiles to determine if the extinct species underwent demographic changes through time that might indicate impaired reproductive capacity or changing patterns of human predation. In sum, as in the case of demonstrating environmental and cultural change from faunal remains, elucidating the causes of extinction is not so much a theoretical problem as it is a practical one of obtaining large, well-excavated, and well-described faunal assemblages from contexts where good data on artefacts, sediments, pollen, and so forth provide controls for comparisons designed to separate the cultural and environmental variables responsible for assemblage composition.

CONCLUSIONS

In the overwhelming majority of cases, it is impossible to assume a one-to-one relationship between the relative abundance of species in a fossil mammal assemblage and their relative abundance in the live community from which they were drawn. Almost always, it is far safer to assume that the agency of accumu-

lation has altered the original frequency relationships, and it is usually impossible to say how much. Thus, for example, the fact that a particular archaeological faunal assemblage consists three-quarters of grazers and one-quarter of browsers does not mean that the grazer/browser ratio in the ancient environment was 3 : 1 or even that grazers were more numerous than browsers. It may be that the people responsible for the bones found it easier to obtain grazers, or that grazers, since they are often larger, provided a higher return for time and effort in the hunt. Whatever the case, the extent to which the people may have altered or 'biased' the original grazer/browser ratio is probably unknowable.

Superficially then, detailed interpretation of fossil mammal assemblages may appear impossible from the outset. However, this is only the case if the goal is to make precise statements about the live abundance of various species or about the subsistence behaviour of people at single instants in past time. It is not true if the focus is on *changes* in live abundance or in cultural practices through time, since, in this case, it is possible to introduce controls for the effects of environment or culture. As an example, take two faunas of different ages from neighbouring archaeological sites or from different levels within the same site. If there is evidence from pollen, sediments, oxygen-isotope ratios in associated marine shells, etc., that the faunas were accumulated under very similar environmental circumstances, it seems reasonable to suppose that any differences in species frequencies between them reflect differences in human behaviour.

Similarly, if there is sound associated evidence for differences in past environment and no artefactual evidence for significant differences in culture, then it is probably most reasonable to conclude that any differences in species frequencies between faunas reflect differences in past environments. As a more concrete example, take two faunas from successive levels in the same site containing broadly similar artefacts, but in sedimentary contexts suggesting important differences in palaeoenvironment. If the fauna of one level contains relatively more grazers than the fauna of the other, it seems most reasonable to conclude that grazers were more common on the hoof at the time the first level formed, even though the live abundance of grazers in the ancient environment of either level remains unknown or unknowable.

Basically then, faunal samples are far more useful for establishing *changes* in environment or culture through time than for reconstructing environments or cultural practices at particular points in time. However, it is obvious that changes may be determined only through comparisons among samples, with controls provided by accompanying pollen, sediments, artefacts, and so forth, as well as by detailed characteristics of the bone assemblages themselves. From this, it follows, first, that faunal analysis is inextricably dependent upon other fields—conventional archaeology, palynology, sedimentology, isotope geo-chemistry, etc.—if interpretations are to be secure. Second, it is obvious that no single sample is ever likely to be very informative. Rather, it is necessary to have many samples to permit as wide a range of controlled comparisons as possible. It is, of course, also important that the samples be large, well described, and well

excavated, to enhance the chances that significant patterns will emerge in the process of comparison.

Among the six southern African ecozones considered in this paper, only the Cape Zone has provided a sufficient number of large, well-described, and well-excavated faunal samples, accompanied by sufficient contextual information, to isolate patterns of mammalian frequency change that probably reflect systematic changes in environment and culture during the Upper Pleistocene and Holocene. The Cape data suggest (i) that Upper Pleistocene intervals of cooler climate locally witnessed the expansion of grass at the expense of fynbos, bush, and forest; (ii) that local Middle Stone Age peoples, living prior to 40 000–30 000 B.P., were less proficient hunter-gatherers than their Later Stone Age successors; and (iii) that a combination of environmental change and the greater hunting proficiency of Later Stone Age peoples was responsible for the extinction of several large mammal species in the Cape Zone 12 000–10 000 B.P. The last two hypotheses are clearly of broad anthropological or evolutionary interest and certainly deserve investigation in other ecozones, as well as further testing in the Cape Zone. Ultimate demonstration of the likelihood that they are correct is not basically a theoretical problem, but a practical one of obtaining numerous large faunal samples from carefully documented contexts.

ACKNOWLEDGEMENTS

A draft of this paper was presented at the Southern African Association of Archaeologists Workshop in Stellenbosch in June 1979. The author thanks K. W. Butzer, J. Deacon, Q. B. Hendey, and T. P. Volman for helpful comments on the draft. The National Science Foundation (Washington) and the Lichtstern Fund of the University of Chicago provided financial support for the author's own research reported here. The research was conducted in facilities kindly provided by the Department of Cenozoic Palaeontology at the South African Museum.

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APPENDIX

VERNACULAR AND SCIENTIFIC NAMES OF THE EXTANT MAMMALIAN SPECIES
MENTIONED IN THE TEXT

VERNACULAR NAME	SCIENTIFIC NAME
hedgehog	<i>Erinaceus frontalis</i>
Cape hare	<i>Lepus capensis</i>
scrub hare	<i>Lepus saxatilis</i>
red rock hare	<i>Pronolagus crassicaudatus</i>
springhare	<i>Pedetes capensis</i>
cane rat	<i>Thryonomys swinderianus</i>
porcupine	<i>Hystrix africae-australis</i>
Cape mole-rat	<i>Bathyergerus suillus</i>
chacma baboon	<i>Papio ursinus</i>
yellow baboon	<i>Papio cynocephalus</i>
vervet monkey	<i>Cercopithecus aethiops</i>
side-striped jackal	<i>Canis adustus</i>
black-backed jackal	<i>Canis mesomelas</i>
Cape hunting dog	<i>Lycaon pictus</i>
spotted hyena	<i>Crocuta crocuta</i>
brown hyena	<i>Hyaena brunnea</i>
lion	<i>Panthera leo</i>
leopard	<i>Panthera pardus</i>
cheetah	<i>Acinonyx jubatus</i>
Cape fur seal	<i>Arctocephalus pusillus</i>
gazelle seal	<i>Arctocephalus gazella</i>
elephant seal	<i>Mirounga leonina</i>
crab-eater seal	<i>Lobodon carcinophagus</i>
rock hyrax	<i>Procavia capensis</i>
tree hyrax	<i>Dendrohyrax arboreus</i>
elephant	<i>Loxodonta africana</i>
Grevy's zebra	<i>Equus grevyi</i>
Burchell's zebra	<i>Equus burchelli</i>
quagga	<i>Equus quagga</i>
mountain zebra	<i>Equus zebra</i>
black rhinoceros	<i>Diceros bicornis</i>
white rhinoceros	<i>Ceratotherium simum</i>
hippopotamus	<i>Hippopotamus amphibius</i>
warthog	<i>Phacochoerus aethiopicus</i>
bushpig	<i>Potamochoerus porcus</i>
giraffe	<i>Giraffa camelopardalis</i>
okapi	<i>Okapia johnstoni</i>
eland	<i>Taurotragus oryx</i>

VERNACULAR NAME	SCIENTIFIC NAME
bongo	<i>Boocercus euryceros</i>
greater kudu	<i>Tragelaphus strepsiceros</i>
nyala	<i>Tragelaphus angasi</i>
sitatunga	<i>Tragelaphus spekei</i>
bushbuck	<i>Tragelaphus scriptus</i>
gemsbok	<i>Oryx gazella</i>
roan antelope	<i>Hippotragus equinus</i>
sable antelope	<i>Hippotragus niger</i>
waterbuck	<i>Kobus ellipsiprymnus</i>
puku	<i>Kobus vardonii</i>
lechwe	<i>Kobus leche</i>
southern reedbuck	<i>Redunca arundinum</i>
mountain reedbuck	<i>Redunca fulvorufula</i>
Cape (= red) hartebeest	<i>Alcelaphus buselaphus</i>
Lichtenstein's hartebeest	<i>Alcelaphus lichtensteini</i>
tsessebe	<i>Damaliscus lunatus</i>
bontebok and blesbok	<i>Damaliscus dorcas</i>
bastard hartebeest	<i>Damaliscus</i> spp.
blue wildebeest	<i>Connochaetes taurinus</i>
black wildebeest	<i>Connochaetes gnou</i>
impala	<i>Aepyceros melampus</i>
Grant's gazelle	<i>Gazella granti</i>
Thomson's gazelle	<i>Gazella thomsoni</i>
springbok	<i>Antidorcas marsupialis</i>
blue duiker	<i>Cephalophus monticola</i>
common (= grey) duiker	<i>Sylvicapra grimmia</i>
oribi	<i>Ourebia ourebi</i>
klipspringer	<i>Oreotragus oreotragus</i>
steenbok	<i>Raphicerus campestris</i>
Sharpe's grysbok	<i>Raphicerus sharpei</i>
Cape grysbok	<i>Raphicerus melanotis</i>
vaalribbok	<i>Pelea capreolus</i>
domestic sheep	<i>Ovis aries</i>
domestic goat	<i>Capra hircus</i>
Cape buffalo	<i>Syncerus caffer</i>
domestic cattle	<i>Bos taurus</i>

6. SYSTEMATIC papers must conform to the *International code of zoological nomenclature* (particularly Articles 22 and 51).

Names of new taxa, combinations, synonyms, etc., when used for the first time, must be followed by the appropriate Latin (not English) abbreviation, e.g. gen. nov., sp. nov., comb. nov., syn. nov., etc.

An author's name when cited must follow the name of the taxon without intervening punctuation and not be abbreviated; if the year is added, a comma must separate author's name and year. The author's name (and date, if cited) must be placed in parentheses if a species or subspecies is transferred from its original genus. The name of a subsequent user of a scientific name must be separated from the scientific name by a colon.

Synonymy arrangement should be according to chronology of names, i.e. all published scientific names by which the species previously has been designated are listed in chronological order, with all references to that name following in chronological order, e.g.:

Family Nuculanidae

Nuculana (Lembulus) bicuspidata (Gould, 1845)

Figs 14-15A

Nucula (Leda) bicuspidata Gould, 1845: 37.

Leda plicifera A. Adams, 1856: 50.

Laeda bicuspidata Hanley, 1859: 118, pl. 228 (fig. 73). Sowerby, 1871: pl. 2 (fig. 8a-b).

Nucula largillierii Philippi, 1861: 87.

Leda bicuspidata: Nickles, 1950: 163, fig. 301; 1955: 110. Barnard, 1964: 234, figs 8-9.

Note punctuation in the above example:

comma separates author's name and year

semicolon separates more than one reference by the same author

full stop separates references by different authors

figures of plates are enclosed in parentheses to distinguish them from text-figures

dash, not comma, separates consecutive numbers

Synonymy arrangement according to chronology of bibliographic references, whereby the year is placed in front of each entry, and the synonym repeated in full for each entry, is not acceptable.

In describing new species, one specimen must be designated as the holotype; other specimens mentioned in the original description are to be designated paratypes; additional material not regarded as paratypes should be listed separately. The complete data (registration number, depository, description of specimen, locality, collector, date) of the holotype and paratypes must be recorded, e.g.:

Holotype

SAM-A13535 in the South African Museum, Cape Town. Adult female from mid-tide region, King's Beach Port Elizabeth (33°51'S 25°39'E), collected by A. Smith, 15 January 1973.

Note standard form of writing South African Museum registration numbers and date.

7. SPECIAL HOUSE RULES

Capital initial letters

- The Figures, Maps and Tables of the paper when referred to in the text
e.g. '... the Figure depicting *C. namacolus* ...'; '... in *C. namacolus* (Fig. 10) ...'
- The prefixes of prefixed surnames in all languages, when used in the text, if not preceded by initials or full names
e.g. Du Toit but A. L. du Toit; Von Huene but F. von Huene
- Scientific names, but not their vernacular derivatives
e.g. Therocephalia, but therocephalian

Punctuation should be loose, omitting all not strictly necessary

Reference to the author should be expressed in the third person

Roman numerals should be converted to arabic, except when forming part of the title of a book or article, such as

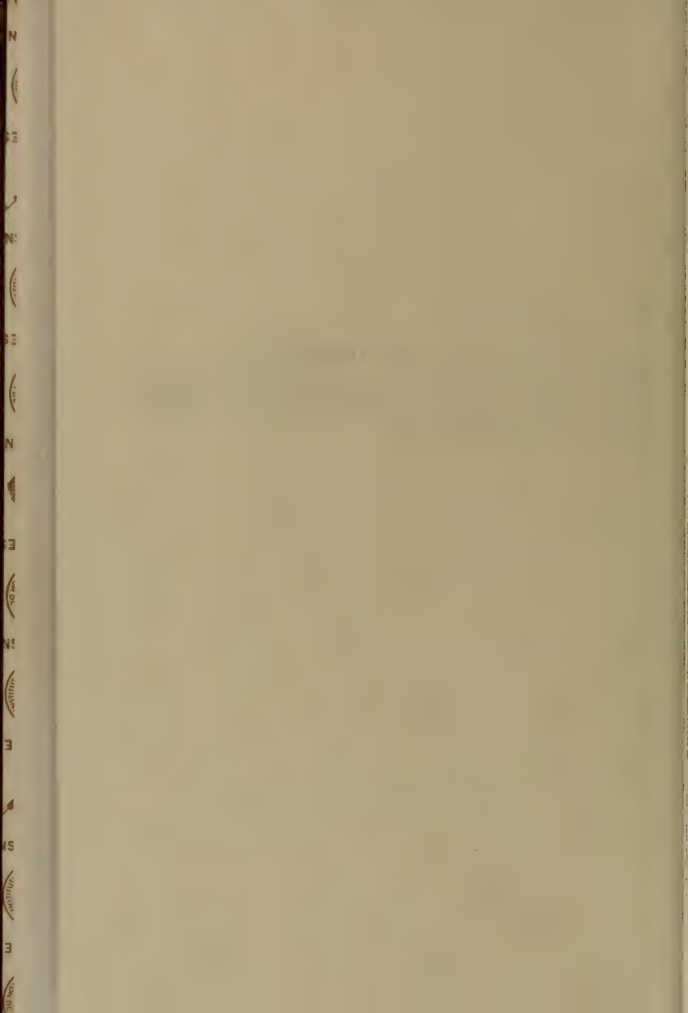
'Revision of the Crustacea. Part VIII. The Amphipoda.'

Specific name must not stand alone, but be preceded by the generic name or its abbreviation to initial capital letter, provided the same generic name is used consecutively.

Name of new genus or species is not to be included in the title: it should be included in the abstract, counter to Recommendation 23 of the Code, to meet the requirements of Biological Abstracts.

RICHARD G. KLEIN

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